Mammals of the Soviet Union

VOLUME I

V. G. Heptner

A. A. Nasimovich

A. G. Bannikov

This volume of *Mammals of the Soviet Union* is devoted to a description of artiodactyls and perissodactyls found in the Soviet Union. These animals are of great scientific and economic interest; information on them, especially in recent Soviet literature, is voluminous. In recent years world literature on this subject has likewise been considerably enriched with new data. The abundance of information on ungulates explains the size of the present volume.

All the characteristics of groups have been described according to a common scheme; deviations occur in a few cases, however. These characteristics are stated briefly and pertain to the group as a whole; they are not exclusive to species of the Soviet fauna. Diagnosis is based essentially on morphology. Considerable attention has been given to the composition of the group, its taxonomic relationships, and the position of Soviet forms in the world fauna.

All species are described according to a common plan, altered only in the case of some extinct forms. In devising the scheme for descriptions of species not only the convenience of the reader was kept in mind, but the hope that gaps in our knowledge would become self-evident and stimulate further research.

(from the Foreword)

Smithsonian Institution Libraries
WASHINGTON, D.C. 20560 202-357-2240

The Smithsonian Institution Libraries has selected your library to receive *gratis* copies of volumes published in our Translations Publishing Program. Under this program, significant non-English-language works that related to a field of Smithsonian research are translated and published with Special Foreign Currency funds according to the provisions of Public Law 480. We hope that you will find this publication a useful addition to your collection. We would appreciate receiving a copy of all reviews of this work.

Additional copies of this work may be purchased from the National Technical Information Service (N.T.I.S.), Springfield, Virginia, 22161. Please cite the TT (Technical Translation) number printed on the Copyright page when ordering from N.T.I.S.

Let us know if your copy of this book is incomplete or damaged.

Please direct all inquiries and address corrections to:

Translations Publishing Program
Smithsonian Institution Libraries
Natural History Building 22
Washington, D.C. 20560

202/357-1850

October 1988

SMITHSONIAN INSTITUTION
WASHINGTON, D.C. 20560
ASSISTANT SECRETARY FOR RESEARCH

June 1990

Dear Colleague:

It is my pleasure to send you a copy of the English edition of Mammals of the Soviet Union, volume 1 (Artiodactyla and Perissodactyla). This basic work, authored by Professor V.G. Heptner and colleagues, first appeared in 1961. It was translated into English by the Smithsonian Institution's Translation Publishing Program, and I served as scientific editor. I hope you will find the book useful to you in your work. It is anticipated that volume 2, part 2 will be published in the near future, followed by volume 2, part 1. I would be happy to hear from you if you believe that these subsequent volumes would be of interest to you.

Sincerely,

Bob

Robert S. Hoffmann
Assistant Secretary
for Research

Mammals of the Soviet Union

Volume I

MAMMALS OF THE SOVIET UNION

In Three Volumes

Edited by
V.G. Heptner and N.P. Naumov

Vysshaya Shkola Publishers
Moscow, 1961

Mammals of the Soviet Union

Volume I

ARTIODACTYLA and PERISSODACTYLA

V.G. Heptner, A.A. Nasimovich
and A.G. Bannikov

Scientific Editor
ROBERT S. HOFFMANN

Smithsonian Institution Libraries
and
The National Science Foundation
Washington, D.C.
1988

TT 76-52040

Mlekopitayushchie Sovetskogo Soyuza
In Three Volumes
V.G. Heptner & N.P. Naumov, editors

Vysshaya Shkola Publishers
Moscow, 1961

Translator: P.M. Rao
General Editor: Dr. V.S. Kothekar

© 1988 Amerind Publishing Co. Pvt. Ltd., New Delhi

Library of Congress Cataloging in Publication Data

Geptner, V.G. (Vladimir Georgievich), 1901–1975.
Mammals of the Soviet Union.

Translation of: Mlekopitaı͡ushchie Sovetskogo Soı͡uza.
Contents: v. 1. Artiodactyla and Perissodactyla.
Supt. of Docs. no.: SI 1.2:Ar7/2
1. Mammals—Soviet Union—Collected works.
I. Nasimovich, A.A. II. Bannikov, Andrei Grigor'evich.
III. Hoffmann, Robert S. IV. Title.
QL728.S65G47 1986 599.0947 85-600144

Translated and published for the Smithsonian Institution Libraries, pursuant to an agreement with the National Science Foundation, Washington, D.C., by Amerind Publishing Co. Pvt. Ltd., New Delhi, India

Printed at Model Press, New Delhi, India

Foreword to the English Edition

Dr. Vladimir Georgievich Heptner, the senior editor and author of *Mammals of the Soviet Union* and Professor at Moscow State University, died in Moscow on 5 July 1975, in his 75th year. Professor Heptner was born in Moscow in 1901. From the day he entered Moscow University as a graduate student in 1919, Professor Heptner's scientific and academic career was indissolubly linked with Moscow University's Faculty of Biology, and with its Zoological Museum. In 1929, he became curator of mammals at the Museum and assistant professor; in 1934, he attained the rank of full professor.

Heptner combined his intensive scientific work with continuous academic activity. Many Soviet biologists, zoogeographers, morphologists, ecologists, and systematists, as well as mammalogists count themselves among his students, and his high esteem among his Soviet colleagues is manifested by their naming about 20 taxa of animals of different classes in his honor. Professor Heptner's scientific and pedagogic activities made him a leader of Soviet zoology and one of the world's most renowned mammalogists. He was one of the oldest members of the Moscow Society of Naturalists and of the Geographical Society of the USSR, and an honorary member of the All-Russian Society of Wildlife Conservation. In 1974, when the Theriological Society of the USSR was founded, he was made its vice-president. His scientific contributions were recognized in many foreign countries: he was an honorary member of the American Society of Mammalogists, the Gesellschaft Naturforschen der Freunde zu Berlin, the Deutschen Gesellschaft für Säugetierkunde, and the Zoological Society of Czechoslovakia. He was also a member of the European Society of Mammal Protection, and of the International Union for Conservation of Nature and Natural Resources.

It is regrettable that during this long and productive career only a small number of non-Soviet mammalogists were fortunate enough to become personally acquainted with his keen mind and breadth of interests. Heptner is best known to American mammalogists for his publications in systematics and zoogeography. He dedicated many years of his life to the problems of zoogeography of the USSR, and of the Holarctic as a whole. In particular, his numerous studies of Middle and Central Asia and Asia Minor, such as his detailed investigations of Old World deserts, and his insights into the role of environment in adaptation and differentiation of desert animals, are of great significance. His contribution to systematics of various mammalian groups is also large. One may note especially his work on systematics of Gerbillinae, a group in which he was especially interested. In the course of his systematic activity, he described about 70 new forms (subspecies, species, and subgenera) of mammals. Evolutionary problems were of the greatest interest to Professor Heptner, especially those of microevolution and subspeciation. He was active not only as a scientist, but a popularizer in the USSR of the polytypic species concept. In this connection, he initiated the translation into Russian of such books as Ernst Mayr's *Systematics and the Origin of Species* (in 1947); *Animal Species and Evolution* (in 1968); *Principles of Systematic Zoology* (in 1971); and *Populations, Species and Evolution* (in 1974); Mayr, Linsely and Usinger's *Methods and Principles of Systematic Zoology* (in 1956); and A. Cain's *Animal Species and their Evolution* (in 1958), all published under his editorship. Professor Heptner also served on editorial boards of various periodicals, including *Zoologicheskii Zhurnal, Doklady Vysshei Shkoly, Okhota i okhotnichie khozyaistvo, Lynx, Das Pelzgewerbe,* and *Säugetierkundliche Mitteilungen.*

An excellent field naturalist, Heptner took part in many expeditions to all parts of the Soviet Union. Under his leadership field parties investigated such diverse areas as the Soviet Arctic, Middle Russia, the northern Caucasus Mountains, Transcaucasia, Turkmeniya, Uzbekistan, the Pamir, the Altai Mountains, and the Soviet Far East. His familiarity with the natural wealth of the USSR, and his appreciation of the problems attendant upon utilization of the country's resources, led him to assume a pioneering role in wildlife conservation. At the same time, his broad approach permitted him to work effectively in "applied" fields such as medical zoology, pest control, fur harvest, and commercial hunting.

Professor Heptner was the author or co-author of about 300 published works, among them such monographs as *Mammals of the Middle Kopet Dagh and Adjacent Plains* (1929), *General Zoogeography* (1963), *Rodents of Middle Asia* (1936), *Vertebrate Animals of Badkhyz* (1956), and *Harmful and Useful Mammals of the Protective Forest Zones* (1950), the latter having been translated into German.

His colleagues, both Soviet and foreign, feel his loss deeply—he was a man of great culture, integrity, fortitude, and generosity, always ready to help anyone with his words and deeds. (Modified from obituary in *J. Mammal.*, 57 (2): 416–417, by Rossolimo and Hoffmann.)

I first met Professor Heptner in May, 1963, two years after the publication of the first volume of wh[illegible]e regarded as his major life work, *Mammals of the Soviet Union.* He considered it to be the successor, and supplement, to S.I. Ognev's *Mammals of the USSR and Adjacent Countries,* a work published in seven volumes between 1928 and 1950. Heptner commenced his series with the ungulates, since Ognev had not lived to complete his task, and this was the major omission. The present volume is thus an invaluable extension of the coverage of Ognev's works. Heptner expressed great concern to me in 1963 that, while Ognev was now being translated into English (the first three volumes had just appeared in 1962, up to thirty-five years after their original publication), they were in many respects out of date. We discussed the desirability of fostering an English edition of his new series, and he expressed the hope that this might be done promptly. Unfortunately, Professor Heptner died in early summer of 1975, and so did not live to see either an English translation of his monograph, or even its completion in Russian; at the time of his death, two parts of volume two had appeared, and a third was posthumously published in 1976. Since then, responsibility for the series has been assumed by Acad. Vladimir E. Sokolov, Director of the Institute of Evolutionary Animal Morphology and Ecology of the Academy of Sciences of the USSR, who assures me that additional volumes will appear in due course.

The English translation project was initiated at my urging in late 1975 as a contribution to joint U.S.–U.S.S.R. studies on the evolution of Holarctic mammals sponsored by the Environmental Agreement between the two countries, and their Academies of Science. The Smithsonian Institution Libraries in cooperation with the National Science Foundation sponsored the translation of this as well as of hundreds of other scientific studies. The Smithsonian Libraries program, funded with Special Foreign Currency under the provisions of Public Law 480, represents an investment in the dissemination of knowledge to which the Smithsonian Institution is dedicated. The translation of volume one was ably completed by P.M. Rao of Amerind Publishing Co., New Delhi, India, under the general editorship of Dr. V.S. Kothekar. I subsequently read the translation in manuscript in order to check for scientific accuracy, and transliteration of proper names.

Geographic names are generally transliterated directly, but a few exceptions were permitted (*e.g.* Moscow instead of Moskva, translation rather than transliteration of certain modifiers of place names, such as Northern, rather than Severnaya, Dvina). Soviet administrative units are numerous, and the following equivalents were employed in translation: *Krai,* territory; *oblast',* district; *raion,* region; *guberniya* (archaic), province. Also, in the original Russian text, rivers, mountain ranges, and cities are often not explicitly identified, the Soviet reader being presumed sufficiently familiar with the geography of the country to be able to understand from the context of the sentence what sort of place is referred to. Complicating the matter is the lack of articles as parts of speech in Russian. To assist the English reader, I have adopted the following conventions: if a river is referred to, an article precedes it; if a mountain range is referred to, it is translated as a plural; if a city is referred to, it is singular, and lacks the article. Examples are: the Ural (river); the Urals (mountains); Ural'sk (city). Geographic place names are also inflected in Russian, and these have been simplified by omitting transliteration of the inflected ending. For example, the Russian phrase *v Yaroslavskoi i Kostromskoi oblastyakh* is translated "in the Yaroslavl and Kostroma districts." In cases where the nominative form of the place name has an -sk ending this is, however, transliterated (*e.g.*, Omsk); when a Russian "soft sign" is employed in a place name, this is transliterated as an apostrophe (*e.g.*, Khar'kov). Because of the large number of place names in this volume, it was not possible to verify all of them, and some inconsistencies are likely to occur. I would appreciate it if readers would bring any errors they may notice to my attention.

Robert S. Hoffmann
Assistant Secretary for Research
Smithsonian Institution
Washington, D.C. 20560

Foreword

5 This volume of *Mammals of the Soviet Union* is devoted to a description of artiodactyls and perissodactyls found in the Soviet Union. These animals are of great scientific and economic interest; information on them, especially in recent Soviet literature, is voluminous. In recent years world literature on this subject has likewise been considerably enriched with new data. The abundance of information on ungulates (more than on other mammals) explains the size of the present volume.

The format and contents of this book require a comment or two. All species of Artiodactyla and Perissodactyla which have ever inhabited the Soviet Union, including those now extinct, are described. Total coverage provides a correct picture of present-day fauna and permits an evaluation of changes in it. Only rhinoceri, information on which is completely fantastic (see text), and the parabubal antelope (a species of Alcelaphinae; Vereshchagin, 1956) have been excluded; their occurrence in Russia in the historic past requires further confirmation.

Simpson's (1945) system, the latest and most comprehensive, has been adopted as the basis for classification. This system covers the entire class down to genera and includes both present-day and fossil forms. True, it has some drawbacks and debatable points but their correction needs extensive investigation, which falls outside the purview of the present work. Hence only relatively insignificant deviations from Simpson's system have been incorporated and mainly concern the number and scope of generic groups. The latter, of course, at least with reference to recent fauna, ought to be delineated in greater detail. The changes introduced here have been defined in the text.

The number of species of artiodactyls, only recently clarified, has been adopted from Haltenorth and Trenze (1956) with minor modifications (oxen, goat, and camel; V.G. Heptner).

All the characteristics of groups have been described according to a common scheme; deviations occur in a few cases, however. These characteristics are stated briefly and pertain to the group as a whole; they are not exclusive to species of Soviet fauna. Diagnosis is based essentially on morphology. Considerable attention has been given to the composition of the group, its taxonomic relationships, and the position of Soviet forms in world fauna. Paleontological references are given, drawn primarily from Simpson's work (1945), but occasionally including other sources as well.

All species are described according to a common plan, altered only in the case of some extinct forms. In devising the scheme for
6 descriptions of species not only the convenience of the reader was kept in mind, but the hope that gaps in our knowledge would become self-evident and stimulate further research.

In describing species geographic distribution and biology are given primary attention. Geographic ranges are presented in general terms (boundaries) based on a critical analysis of the factual material available. Stray occurrences outside the frontiers of the range are usually not included and only the main reference points of the range boundary indicated.

Descriptions are based on "reconstructed" geographic ranges for the historic past, the dynamics of which have been traced insofar as possible. This approach evolved from the conviction that present-day ranges and modern faunal complexes cannot be understood without reconstruction of earlier ranges. Without such a historic perspective, present-day ranges often give an altogether distorted picture of the zoogeographic and ecological features of present-day species and the composition of extant fauna. Furthermore, a reconstructed range provides an excellent basis for undertaking practical measures (acclimatization and reacclimatization).[1] Geographic ranges falling within the USSR have been detailed to the best of our ability but sometimes minor variations in time and space could not be traced. By and large the widest spread of species (in a given interval of time or in general) has been considered.

In those cases where the geographic range underwent significant changes, beyond the magnitude of normal boundary variations, these have been traced and described as completely as possible. This phenomenon is extremely interesting both from theoretical and economic points of view. Only very general remarks are made concerning the geographic ranges in the prehistoric period and the Pleistocene. All the geographic range maps are original and were plotted from material collected for this publication.

Geographic ranges falling outside the USSR, including reconstructed ones, are highly schematic and based on a large number of special studies and important compilations: Seton (1909–1910);

---

[1] For further details on reconstructed geographic ranges, see V.G. Heptner's work: Dinamika areala nekotorykh mlekopitayushchikh i antropicheskii faktor (Dynamics of geographic range of some mammals and the human factor). Sb. *Voprosy Geografii,* 1959.

Miller (1912); Lydekker (1913–1916); Sowerby (1923); Anthony (1928); Shortridge (1934); Philips (1935); Heim de Balzac (1936); Allen (1939, 1938–1940, 1942); Cabrera and Yepes (1940); Chasen (1940); Rode (1943–1944); Harper (1945); Simpson (1945); Anderson (1946); Tate (1947); Prater (1947); Hainard (1949); Roberts (1951); Ellerman and Morrison-Scott (1951); Burt and Grossenheider (1952); Morrison-Scott and Hayman (1953); Miller and Kellog (1955); Haltenorth and Trenze (1956); Van den Brink (1958); and others (for which references have been given in the text).

The morphological characters of species are very briefly stated since detailed descriptions are available for most in Soviet literature (deer, cavicorns, sheep, goats, and others). Only species found within the Soviet Union are described; however, the taxonomic position of each has been assessed within the genus as a whole. Geographic variation in the USSR has been revised or critically reviewed. Forms inhabiting the USSR have, by and large, been drawn from the most recent compilations of mammalian species in the Soviet Union.

A strictly limited number of synonyms are included, based on the following principles. Only natural synonyms are mentioned. For genera synonyms are presented only for those for which the Soviet forms serve as the type genus, or if the generic name is important, or is sometimes used (or was formerly used), or could be applied to Soviet species. All names, current or otherwise, have been included among the synonyms of a species in the following cases: 1) name assigned from specimens of a species found in Soviet territory; 2) name given from specimens of a species belonging to other territories, but important and used or formerly used but persisting for some Soviet forms; 3) name given for specimens belonging to other territories, not used for Soviet forms but possibly relevant for 7 some; and 4) name of nominal form invariably given irrespective of its type locality (whether within or outside the USSR). Current names have not been separately identified among the synonyms of a species, but are included in the list of subspecies inhabiting the USSR where synonyms pertaining to a given subspecies are also indicated. Synonyms of subspecies occurring outside the USSR have been excluded. Synonyms for categories above genus have not been mentioned; neither have references to their description and nomenclature or, if mentioned, only those based on Simpson's system. Names given for domestic forms (horses, goats, etc.) have not been used here for wild species; the first name given to the wild form is used as its species name. Descriptions of species within an order commence with the least specialized one.

The total number of mammalian species is approximately 3,500 and the number of species in Soviet fauna about 300 (Heptner, 1956).

In the preparation of this book each author contributed as follows: V.G. Heptner has written the introduction, characteristics of groups, including generic, keys for identification, all of the chapter devoted to aurochs*, yaks, and tarpans, and the sections "Diagnosis," "Description," "Geographic Distribution," and "Geographic Variation" for all species except goitered gazelle. Mongolian gazelle, and saiga. He also processed the synonyms for all genera and species. A.A. Nasimovich has written the sections "Biology" and "Economic Importance" for all species of artiodactyls except swine, aurochs, yak, gazelle, antelope, and saiga. A.G. Bannikov compiled the descriptions, apart from synonyms and geographic variation (described by V.G. Heptner) of saiga, goitered and Mongolian gazelles, and the sections "Biology" and "Economic Importance" of hog and wild ass. The authorship of some individual sections has been acknowledged in the form of author initials at the end of the corresponding section or chapter. V.G. Heptner is responsible for the classification adopted for the majority of the species, subspecies, etc.

Literature of 1956 and 1957 and partly 1958 has been included. From the works of 1959 only some articles were included during editorial revision. The bibliography contains only cited works; the literature actually perused was naturally more extensive. Works referred to in giving synonyms of species and genera and those not used subsequently in the text have not been included in the bibliography.

In the compilation of this monograph the authors naturally included in the text (in some cases acknowledged) their unpublished material. Moreover, a significant amount of unpublished data furnished by various authors has been included, namely: K.G. Abramov (Ussuri); Yu.V. Averin (Kishinev); I.I. Barabash-Nikiforov (Voronezh); O.P. Bogdanov (Tashkent); G.F. Bromlei (Vladivostok); I.V. Zharkov (Voronezh preserve); M.A. Zablotskii (Prioksko-Terras preserve); Yu.A. Isakov (Moscow); F.L. Ivanauskas (Kaunas); P.F. Kaznevskii (Voronezh preserve); S.G. Kalugin (Caucasian preserve); V.P. Kostin (Tashkent); V.A. Kotov (Caucasian preserve); L.S. Lebedeva (Moscow); A.N. Leont'ev (Chita); R.N. Meklenburtsev (Tashkent); K.D. Mamisashvili (Lagoda preserve); P.A. Merttsem

---

*Some confusion exists in the Russian original with regard to turs (mountain goats) and aurochs—General Editor.

(Caucasian preserve); B.M. Petrov (Tashkent); A.S. and I.F. Popkov (Zakatal'sk preserve); P.P. Tarasov (Przheval'sk); V.V. Timofeev (Irkutsk); O.I. Semenov-Tyan-Shanskii (Lapland preserve); V.N. Skalon (Irkutsk); A.V. Fedosov (Bryansk); V.I. Chernyshev (Stalinabad); F.D. Shaposhnikov (Tyumen); P.B. Yurgenson (Moscow); and several others (acknowledged at the appropriate place).[2]

Workers in almost all of the regional game inspectorates to whom requests were sent for information about the distribution of various species responded readily. Extremely informative material was furnished by comrades Starodubchenko (Kur'); Lebedov (Stalingrad); Mikhaylovka (Saratov); Zakharov (Murmansk); Gusev 8 (Rostov-on-Don); Khmelevskii (Orenburg); Sukhikh (Belgorod); Ivanov (Yakutia); Kuz'min and Fofanov (Novosibirsk); Bel'skii (Vladivostok); Anashkin (Ulan Ude); Samsonov (Blagoveshchensk); Sysoev (Khabarovsk); and Zimin (Chita). Some material was provided by N.V. Eliseev, Director of the Central Board of Hunting and Preserves, Russian Soviet Federated Socialist Republic.

Valuable unpublished material on distribution—references, maps, manuscripts, etc.—was furnished by V.Ya. Parovshchikov (Arkhangel'sk); K.A. Tatarinov (L'vov); A.P. Korneev (Kiev); and A.A. Sludskii (Alma-Ata); and especially by N.K. Vereshchagin (Leningrad) and S.V. Kirikov (Moscow). The authors express their deep gratitude to each and everyone of them, as well as to S.P. Naumov and S.S. Turov who reviewed the manuscript and offered several suggestions.

The authors are also extremely indebted to V.N. Aleksandrov, V.A. Kotov, E.P. Knorr, G. Levenshtein, K.T. Yurlov, P.A. Yanushko, O.I. Semenov-Tyan-Shanskii, Yu.V. Averin, V.D. Treus, and several others whose names have been given at appropriate places. The authors are grateful for various illustrative material to H. Heck, Director of Munich Zoological Garden, who furnished a photograph of his reconstructed auroch and tarpan. V.A. Dolgov and V.N. Orlov rendered invaluable assistance in the preparation of the manuscript for the printer.

The authors received much cooperation in various forms from the Zoological Museum of Moscow University; the present volume is largely based on material provided by the university.

In a work of such magnitude and extensive literary coverage, errors and omissions in information are inevitable. This is particularly so for data on distribution. How vague our knowledge still is, is evident in the distribution of argali sheep in Turkmenia, Gissar, and Zerevshan mountains. The authors request all readers, especially folklorists, hunters, and other specialists to send their comments, corrections, and supplementary information to Prof. Vladimir Georgievich Heptner, Zoological Museum, Moscow University, Hertsen Street, 6, Moscow, K-9.

---

[2] To differentiate references to literature, references to personal communications have been identified by including the initials of the author and omitting the year.

Table of Contents*

FOREWORD TO THE ENGLISH EDITION v

FOREWORD ix

CLASSIFICATION OF CLASS MAMMALIA xxv

KEY FOR IDENTIFYING ORDERS OF MAMMALS xxvi

PART I. ORDER OF EVEN-TOED UNGULATES ORDER ARTIODACTYLA OWEN, 1848

- Superorder Paraxonia Marsh, 1884 3
  - Order Artiodactyla Owen, 1848 3
    - Suborder Suiformes Jaeckel, 1911 11
      - Infraorder Suina Gray, 1868 15
        - Family Suidae Gray, 1821 (Swine) 15
          - Boar, or Wild Swine: Genus *Sus* Linnaeus, 1758 16
            - 1. *Sus (Sus) scrofa* Linnaeus, 1758 19
              - Diagnosis 20
              - Description 20
              - Taxonomy 25
              - Geographic Distribution 26
              - Geographic Variation 43
              - Biology 45
              - Economic Importance 78
    - Suborder Tylopoda Illiger, 1811 83
    - Suborder Ruminantia Scopoli, 1777 85
      - Infraorder Pecora Linnaeus, 1758 91
        - Superfamily Cervoidea Simpson, 1931 91
          - Family Cervidae Gray, 1821 91

---

*Pages 773–776 in Russian original. The English table of contents is not a literal translation.

Subfamily Moschinae Zittel, 1893 (Musk Deer) 98

Genus of Musk Deer: Genus *Moschus* Linnaeus, 1758 100

2. *Moschus moschiferus* Linnaeus, 1758 101

Diagnosis 101

Description 101

Taxonomy 105

Geographic Distribution 105

Geographic Variation 111

Biology 112

Economic Importance 122

True or Plesiometacarpal Deer 124

Subfamily Cervinae Baird, 1857 124

Genus of True Deer: Genus *Cervus* Linnaeus, 1758 126

3. Spotted [sika] deer: *Cervus (Cervus) nippon* Temmink, 1838 131

Diagnosis 132

Description 132

Taxonomy 136

Geographic Distribution 136

Geographic Variation 141

Biology 141

Economic Importance 156

4. True, Wellborn [Red] Deer: *Cervus (Cervus) elaphus* Linnaeus, 1758 159

Diagnosis 161

Description 162

Taxonomy 167

Geographic Distribution 167

Geographic Variation 185

Biology 190

Economic Importance 230

Subfamily of Elk, or Telometacarpal Deer: Subfamily Odocoileinae Pocock, 1923 235

Genus of Roe Deer: Genus *Capreolus* Gray, 1821 238
- 5. Roe Deer: *Capreolus capreolus* Linnaeus, 1758 243
  - Diagnosis 244
  - Description 244
  - Taxonomy 249
  - Geographic Distribution 249
  - Geographic Variation 275
  - Biology 280
  - Economic Importance 299

Genus of Elk: Genus *Alces* Gray, 1821 302
- 6. Elk, *Sokhatyi*: *Alces alces* Linnaeus, 1758 307
  - Diagnosis 308
  - Description 309
  - Taxonomy 314
  - Geographic Distribution 314
  - Geographic Variation 358
  - Biology 363
  - Economic Importance 417

Genus of Reindeer: Genus *Rangifer* H. Smith, 1827 425
- 7. Reindeer: *Rangifer tarandus* Linnaeus, 1758 430
  - Diagnosis 432
  - Description 432
  - Taxonomy 438
  - Geographic Distribution 438
  - Geographic Variation 458
  - Biology 463
  - Economic Importance 512

Superfamily of Hollow-horned Ungulates: Superfamilia Bovoidea Simpson, 1931 519

Family of Hollow-horned Ungulates, or Cattle: Familia Bovidae Gray, 1821 519

Subfamily Bovinae Gill, 1872 (Cattle) 532

Genus of Aurochs, or True Cattle: Genus *Bos* Linnaeus, 1758 (Cattle) 537

- 8. Aurochs, Primitive Cattle: *Bos (Bos) primigenius* Bojanus, 1827 539
- 9. Yak: *Bos (Poëphagus) mutus* Przevalski, 1883 549

Genus of Zubr [= Wisent]: Genus *Bison* H. Smith, 1827 554

- 10. Wisent: *Bison bonasus* Linnaeus, 1758 557
    - Diagnosis 558
    - Description 558
    - Taxonomy 560
    - Geographic Distribution 561
    - Geographic Variation 571
    - Biology 573
    - Economic Importance 598

Subfamily of Gazelles: Subfamily Antilopinae Baird, 1857 599

Genus of Gazelles: Genus *Gazella* Blainville, 1816 604

- 11. Dzheiran: *Gazella subgutturosa* Gueldenstaedt, 1780 608
    - Diagnosis 608
    - Description 608
    - Taxonomy 610
    - Geographic Distribution 610
    - Geographic Variation 617
    - Biology 617
    - Economic Importance 632

Genus of Dzeren, or Mongolian Antelope (Gazelle): Genus *Procapra* Hodgson, 1846 634

- 12. Mongolian Gazelle, or Dzeren: *Procapra gutturosa* Pallas, 1777 636
    - Diagnosis 637
    - Description 637
    - Taxonomy 639
    - Geographic Distribution 639

Geographic Variation 642
Biology 642
Economic Importance 652
Subfamily of Goats: Subfamily Caprinae Gill, 1872 653
Genus of Saiga: Genus *Saiga* Gray, 1843 659
13. *Saigak,* Saiga: *Saiga tatarica* Linnaeus, 1766 662
Diagnosis 662
Description 662
Taxonomy 666
Geographic Distribution 666
Geographic Variation 671
Biology 672
Economic Importance 696
Genus of Gorals: Genus *Nemorhaedus* H. Smith, 1827 700
14. Goral: *Nemorhaedus goral* Hardwicke, 1825 704
Diagnosis 705
Description 705
Taxonomy 707
Geographic Distribution 707
Geographic Variation 711
Biology 713
Economic Importance 719
Genus of Chamois: Genus *Rupicapra* Blainville, 1816 (Chamois) 720
15. Chamois, *Serna,* Black Goat: *Rupicapra rupicapra* Linnaeus, 1758 723
Diagnosis 724
Description 724
Taxonomy 727
Geographic Distribution 728
Geographic Variation 732
Biology 734

Economic Importance 746

Genus of Mountain, or Rock, Goats: Genus *Capra* Linnaeus, 1758 748

16. Bearded or Bezoar Goat: *Capra (Capra) aegagrus* Erxleben, 1777 756
    - Diagnosis 757
    - Description 757
    - Taxonomy 760
    - Geographic Distribution 761
    - Geographic Variation 766
    - Biology 768
    - Economic Importance 773
17. Siberian Mountain or Rock Goat [Siberian Ibex]: *Capra (Capra) sibirica* Pallas, 1776 774
    - Diagnosis 775
    - Description 775
    - Taxonomy 784
    - Geographic Distribution 785
    - Geographic Variation 795
    - Biology 798
    - Economic Importance 814
18. Kuban Tur: *Capra (Capra) caucasica* Gueldenstaedt and Pallas, 1783 816
    - Diagnosis 817
    - Description 817
    - Taxonomy 822
    - Geographic Distribution 823
    - Geographic Variation 825
    - Biology 826
19. Dagestan Tur: *Capra (Capra) cylindricornis* Blyth, 1841 826
    - Diagnosis 826
    - Description 826
    - Taxonomy 831
    - Geographic Distribution 833
    - Geographic Variation 837

Biology 838
Economic Importance 857
20. Screw-horned Goat or Markhor: *Capra (Orthaegoceros) falconeri* Wagner, 1839 859
Diagnosis 859
Description 860
Taxonomy 863
Geographic Distribution 864
Geographic Variation 868
Biology 870
Economic Importance 874
Genus of Mountain, or Rock, Sheep: Genus *Ovis* Linnaeus, 1753 874
21. Mountain Sheep, Arkhar: *Ovis ammon* Linnaeus, 1758 881
Diagnosis 884
Description 884
Taxonomy 902
Geographic Distribution 903
Geographic Variation 919
Biology 929
Economic Importance 952
22. Snow Sheep, Bighorn Sheep, Chubuk: *Ovis canadensis* Shaw, 1804 954
Diagnosis 955
Description 955
Taxonomy 959
Geographic Distribution 959
Geographic Variation 965
Biology 969
Economic Importance 978
SUPPLEMENT TO ORDER OF EVEN-TOED UNGULATES 981

ARTIODACTYLA 981
  Deer Family 981
    Family Cervidae Gray, 1821 981
      Genus of True Deer: Genus *Cervus* Linnaeus, 1758 981
        23. Fallow Deer: *Cervus (Dama) dama* Linnaeus, 1758 981
          Diagnosis 981
          Description 981
          Taxonomy 984
          Geographic Distribution 985
          Geographic Variation 989
          Biology 990
          Economic Importance 994

PART II. ORDER OF ODD-TOED UNGULATES
ORDER PERISSODACTYLA OWEN, 1884

Superorder Mesaxonia Marsh, 1884 997
  Order Perissodactyla Owen, 1848 997
    Suborder of Horses: Suborder Hippomorpha Wood, 1937 1005
      Superfamily Equoidea Hay, 1902 1005
        Family Equidae Gray, 1821 1005
          Subfamily Equinae Steinmann and Döderlein, 1890 1009
            Genus of Horses: Genus *Equus* Linnaeus, 1758 1009
              1. Kulan: *Equus (Equus) hemionus* Pallas, 1775 1011
                Diagnosis 1012
                Description 1012
                Taxonomy 1014
                Geographic Distribution 1015
                Geographic Variation 1023
                Biology 1025
                Economic Importance 1036

2. Tarpan: *Equus (Equus) przewalskii* Poljakov, 1881 1037
Diagnosis 1039
Description 1039
Taxonomy 1041
Geographic Distribution 1041
Geographic Variation 1046
Biology 1051
Economic Importance 1055

LITERATURE CITED 1059

INDEX OF LATIN NAMES OF TAXA* 1135

---

*The Russian original also included an Index of Russian Names of Taxa, omitted here.

Classification of Class Mammalia

9 The main taxonomic subdivisions (up to orders) adopted in the present work are based on the monograph on taxonomy written by G.G. Simpson (1945), who made extensive use of paleontological data. It is very similar to the system developed by M. Weber (1928), which, in its time, was well founded on anatomical data of recent forms. The orders acknowledged by Simpson have long been recognized and their grouping as suggested by him into higher groups gives rise to no serious objections.

Of late a tendency has developed for greater fragmentation of orders. It has been proposed that marsupials be divided into three orders (Polyprotodontia, Caenolestoidea, and Diprotodontia), cetaceans into two orders (toothless whales—Mystacoceti, and toothed whales—Odontoceti), primates into three orders (Prosimiae, Simiae, and Tarsioidea), and so on. All these suggestions, however, are as yet not well founded. Moreover, among the morphology and paleontology oriented mammalian systematists such a tendency to extreme division is not acceptable. We believe an order is primarily an integrating and not a differentiating concept. Otherwise the same situation will inevitably arise in mammalogy as has already arisen in ornithological taxonomy wherein the concept of an order has largely lost its meaning; as a result the scientific aspect of vertebrate systematics has suffered greatly.

Only one change has been made in the orders under consideration—pinnipeds are treated as an independent order and not as a suborder of Carnivora. Based on the classification of modern mammals these two groups separate naturally, i.e., they are no less distinctive than some other orders.

Based on already established views Lagomorpha are treated as a separate order (Weber considered them only a suborder of rodents). Thus, instead of the 18 orders of Simpson, 19 are recognized here. Of these, 10 (52.6%) are represented in Soviet fauna and one (Steller's sea cow) is now extinct.

The classification adopted for the class is depicted below. Orders present in the Soviet fauna are asterisked (V.H.).

10 CLASS MAMMALIA

Subclass PROTOTHERIA		Order MONOTREMATA
Subclass THERIA		
Infraclass METATHERIA		Order MARSUPIALIA
Infraclass EUTHERIA		
Cohort UNGUICULATA		*Order INSECTIVORA Order DERMOPTERA *Order CHIROPTERA Order PRIMATES Order EDENTATA Order PHOLIDOTA
Cohort GLIRES		*Order LAGOMORPHA *Order RODENTIA
Cohort MUTICA		*Order CETACEA
Cohort FERUNGULATA	Superorder FERAE	*Order CARNIVORA *Order PINNIPEDIA
	Superorder PROTUNGULATA	Order TUBULIDENTATA
	Superorder PAENUNGULATA	Order PROBOSCIDEA Order HYRACOIDEA *Order SIRENIA
	Superorder MESAXONIA	*Order PERISSODACTYLA
	Superorder PARAXONIA	*Order ARTIODACTYLA

11 *Key for identifying Orders of Mammals*

1 (2). Hind limbs absent. Body fishlike with large bilobate caudal fluke set horizontally .... CETACEA

2 (1). Hind limbs present. Body not fishlike; tail, if present, not in form of bilobate fluke.

3 (4). Forelimbs in form of leathery wings .. CHIROPTERA

4 (3). Forelimbs of different structure.

5 (6). Fore- and hind-limbs very short, paddle-shaped, and in the form of fins, i.e., all digits right up to very tips enclosed in a common skin .... PINNIPEDIA

6 (5). Fore- and hind-limbs of different structure, not in form of fins.

7 (10). Hooves on feet.

8 (9). Only one hoof on each limb .... PERISSODACTYLA

9 (8). Two large hooves and two small ones set above them occur on each limb .... ARTIODACTYLA[1]

10 (7). Hooves absent on legs (claws present).

11 (14). Diastema occurs between large, chisellike incisors and molars; its length not less than length of entire row of molars on corresponding jaw.

12 (13). Two incisors on upper jaw .... RODENTIA

13 (12). Four incisors on upper jaw; small blunt one occurs behind each of two large sharp ones .... LAGOMORPHA

14 (11). Diastema between incisors and molars absent or much smaller than length of molar row. Canines present.

15 (16). Anterior portion of snout extends into well-developed small proboscis. Anteriormost tooth on each jaw or only on upper jaw much larger than adjacent tooth.[2] ... INSECTIVORA

16 (15). Anterior portion of snout does not form proboscis. Anteriormost tooth on each jaw not larger than adjacent one ... . CARNIVORA[3]

(V.H.)

---

[1] Structure of limbs differs in camels. Each limb ends in two broad callused pads and true hooves absent; replaced with two very broad claws. Camels are not included in this key because they are domesticated animals.

[2] If tooth relation differs, proboscis always present and anteriormost tooth extremely short. Wrist very broad with huge claws and set on edge—inner surface backward (moles).

[3] Skulls of extinct Steller's cow, a representative of the order of sea cows or Sirenia, have been found on the coast of Commander Islands. They are distinguished by the absence of teeth on either the upper or lower jaw over a length of about 60 cm.

PART I

ORDER OF EVEN-TOED UNGULATES

Order Artiodactyla Owen, 1848

Superorder PARAXONIA Marsh, 1884

Order ARTIODACTYLA Owen, 1848

15 Artiodactyla is one of the most specialized orders of terrestrial mammals and includes large, medium, and rarely, small-sized species, most of which are light in build and only a few heavy and bulky.

The digits on the fore- and hind limbs generally number four, but in some cases two or four in the fore-limbs and three in the hind limbs. Correspondingly, but to varying degrees, other metapodial elements also undergo reduction. The limb axis invariably passes between digits III and IV (paraxonic), which are better developed than the other digits and carry the entire body weight in most cases. As a result of the great development (elongation) of the axial portion of the metapodium, the lateral digits are not only smaller than the medial but also set above them. The terminal phalanges of the digits are hooved and asymmetrical in shape. The terminal phalanges of the medial digits are greatly enlarged. Some have an enlarged toenail instead of a hoof.

As a result of adaptation to fast running, all the limb sections in most of these animals are highly elongated. Simultaneously, diversity of movement (pronation and supination) was lost and confined to movement of the entire limb and bending and unbending of its component parts in a sagittal plane. Both the clavicle and the third trochanter of the femur absent. In most animals of this order the ulna is reduced and fused with the radius. Fibula either not fully developed or fused with the tibia. The astragalus has two (upper and lower) articular surfaces. There are usually 19 thoracicolumbar vertebrae. The tail in most animals is greatly reduced and either almost invisible externally or barely so; in other animals (oxen) it is quite long.

As a result of the elongation of teeth and the tooth row, the skull usually has a protruding facial portion, sometimes elongated in the form of a wedge; a tendency toward pneumatization of individual bones is seen to some extent. The orbit is separated from the temporal fossa by the fused postorbital processes of the frontal and jugal bones, or these processes are not fused and a gap occurs between them. The lacrimal is well developed and its facial and orbital portions equal in size or the former greatly reduced. In some animals a
16 well-developed ethmoid pit occurs before the lacrimal. The alisphe-

noid canal is not developed. In most species horns are present in one or both sexes. With few exceptions,[1] the horns are a single pair and set on a projection of the frontal. The horns are bony and renewed annually or permanent[2], consisting of horny material around a bony core.

Dentition is heterodont and diphyodont. The complete dental formula is:

$$i\frac{3}{3},\quad c\frac{1}{1},\quad pm\frac{4}{4},\quad m\frac{3}{3} = 44.$$

However, a great reduction in teeth is seen in most artiodactyls; the upper incisors, canine, and first premolar are absent, and the lower canine generally incisiform. The diastema is usually distinct, the tooth row extended, and the molars bluntly tubular (bunodont in a few) or selenodont, or brachyodont more often hypsodont, and sometimes prismatic.

The stomach in most artiodactyls is complex (ruminant) and consists of several chambers; rarely, it is simple. The cecum varies in design or is even absent. In most species distinct aggregations of cutaneous glands are present. The hair coat generally consists of normal hair, usually very coarse, but is sometimes bristly or almost absent. Inguinal teats number one or two pairs commonly. In some forms (pigs), however, five or six pairs of inguinal and abdominal teats are present. The scrotum is usually well developed and absent only exceptionally (*Hippopotamus* and *Sus*) (testes here lie under the skin). The uterus is bicornuate and the placenta diffuse or polycotyledonary. Sexual dimorphism is often well marked and in some animals associated with season or age.

In structure, external appearance, size, and biological characteristics, artiodactyls are extremely diverse and represented by well-known types such as pigs, hippopotami, camels, llamas, mouse-deer, musk deer, giraffes, oxen, goats, sheep, and the highly diverse group "antelopes". The largest forms (giraffes) have a body length of almost 5 m, overall height of up to 6 m, height at withers up to 3 m or slightly more (3.3 m) or (hippopotami) a body length of up to 4.5 m, height at withers up to 1.5 m, and weight up to 2,650 kg. The smallest forms (*Neotragus*) have a height at withers of 25 cm, total body length up to 52 cm, and weight 2 to 3 kg.

---

[1] *Tetraceros* has four typical horns. *Giraffa* has two, three, or five horns set not only on the frontal but also on the parietal and nasal bones; no bony or horny portion is exposed in them.

[2] *Antilocapra* (American pronghorn) is an exception.

Most artiodactyls are swift runners and some are well adapted to scaling cliffs. As a result, most are slender in general appearance and have long legs. They live in diverse environments—forests of all types (from humid tropical to elfin woodlands), shrub growths, steppes, deserts, tundras, marshes, and reed bushes at all altitudes right up to the tops of extremely high mountains. One genus (*Hippopotamus*) leads an amphibious mode of life.

These animals usually live in herds or in small groups and are rarely found singly. They do not construct shelters nor maintain permanent shelters. Many species perform seasonal or irregular migrations, often over considerable distances. They are predominantly polygamous, and usually bear one or two offspring, rarely four, five, or seven, and in a few species up to ten and perhaps twelve. The young are highly developed at birth and soon able to run. Males do not participate in the care of the offspring.

Most artiodactyls are strict herbivores and eat mainly grassy vegetation and rarely shrubs or trees and more rarely aquatic vegetation. A few species exhibit a euryphagous tendency and consume vegetative as well as animal food—mainly terrestrial and soil invertebrates and sometimes small vertebrates.

Artiodactyls are characterized by extremely wide distribution. They are found in South America (from Tierra del Fuego), throughout all of North America, including the Arctic archipelago and
18 Greenland (of the Aleutians evidently only Unimak), all of Africa, Madagascar, and Eurasia, in the north including Spitsbergen (absent in Iceland), Novaya Zemlya, the southern island of Severnaya Zemlya, and New Siberian Islands (absent on Wrangel Island and on all Kuril Islands except probably Shumsha). In the south, the geographic range covers Ceylon, Nicobar and Andaman Islands, and the entire island region between Asia and Australia in the south, including Little Sunda Islands, Timor, Aru and Kai archipelagos, New Guinea, and Louisiade and Solomon Islands (reconstructed range).[3]

In diversity of form and biological types, geographic distribution, and number of species and population size artiodactyls constitute the most prosperous group of ungulates.

Modern artiodactyls have been grouped with perissodactyls (and placed in the same superorder). In reality these two groups are morphologically widely separated, and as far as can be judged from

---

[3] Sambar on Guam Island (Mariana Islands) is an acclimatized Philippine species (*Rusa philippinensis*).

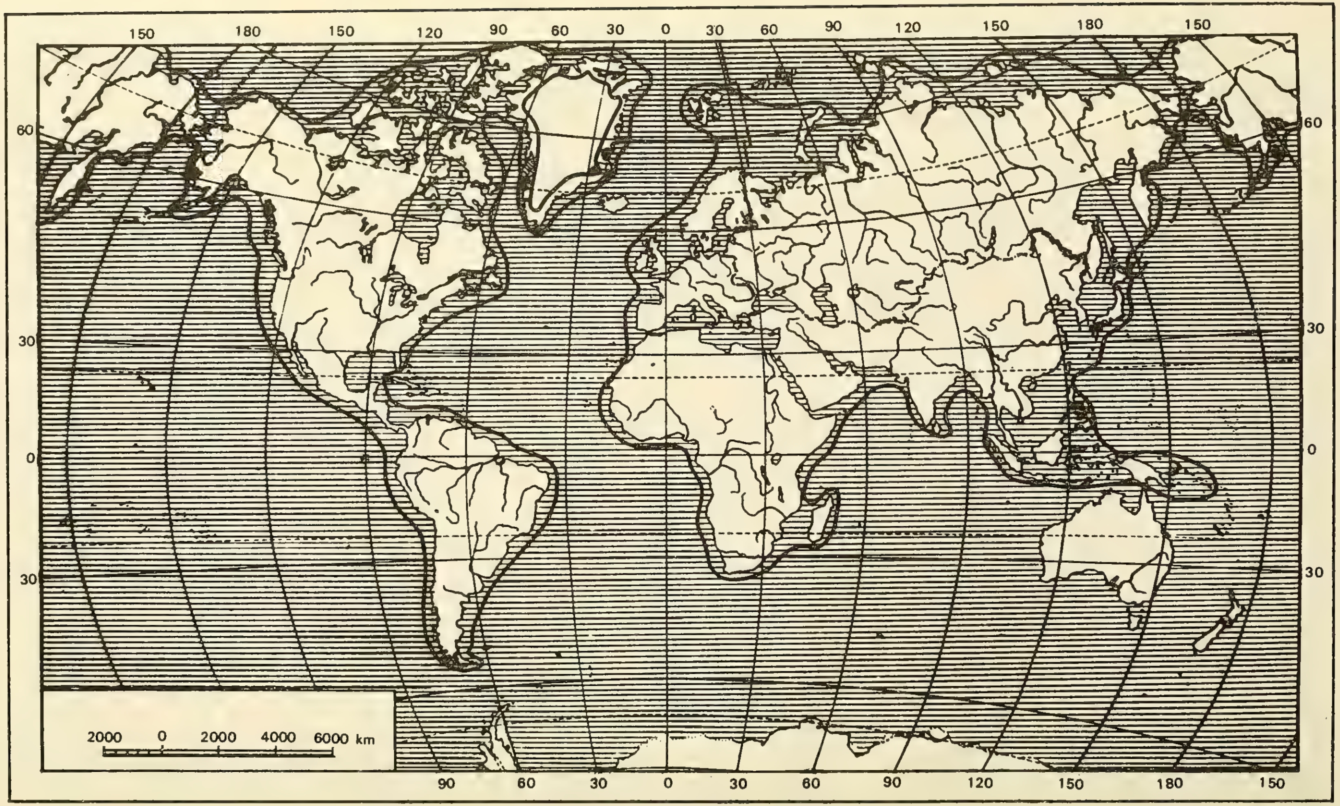

150
180
150
120
90
60
30
0
30
60
90
120
150
180
150
60
30
0
30
2000
0
2000
4000
6000 km

Fig. 1. Geographic distribution of order Artiodactyla (scale in km). Boundaries of reconstructed range. V.G. Heptner.

paleontological material, cannot be regarded as closely associated phylogenetically. The phylogenetic relationship of artiodactyls with perissodactyls is not much closer than their relationship with carnivores, and even less than the relationship between hyraxes, sirenians, and elephants. In the latest taxonomic systems the separation of artiodactyls and perissodactyls is emphasized by assigning to each group the rank of superorder (Paraxonia and Mesaxonia). They are linked only within the cohort Ferungulata, which also includes carnivores, pinnipeds, hyraxes, elephants, and sirenians (Simpson, 1945). Differences in their parasitic fauna also underscore the distinct segregation of artiodactyls and perissodactyls. Several features of similarity between the two orders evidently arose through parallel evolution associated with adaptation to swift running and feeding on coarse, partly dry, herbaceous food.

Remains of ungulates have not been found in Cretaceous formations. Fairly diverse and widely-distributed ungulate faunas of the extinct orders Condylarthra, Amblypoda, and Notoungulata have been found at the commencement of the Tertiary period (Paleocene). Evidently ungulates developed from primitive placentals in the Upper Mesozoic. Artiodactyls appear in Lower Eocene formations of North America and Europe. One has to search among Condylarthra for ancestors of artiodactyls as for some other groups of recent ungulates. Condylarthra are closely associated with primitive carnivores (extinct Creodonta).

Perissodactyls were already well-developed in the Lower Eocene. Both groups appeared simultaneously, probably from the same stock. In Lower Tertiary horizons artiodactyls were fewer numerically than perissodactyls. This ratio gradually changed later. Artiodactyls, mainly Ruminantia, began to increase numerically and in the Upper Tertiary period formed the predominant group of ungulates. This ratio persists even to the present day.

The classification of artiodactyls presents considerable difficulties, mainly because of the large number and diversity of forms. The problem is further complicated when fossil forms are also taken into consideration. Hence the systems of classification proposed by different authors vary greatly. It is rational to adopt three suborders—Suiformes, Tylopoda, and Ruminantia. All fossil forms also fit into these suborders.

The order Artiodactyla comprises 419 genera included in 25 families, of which 16 are extinct and 9 extant; extinct genera number 333 and extant 86 (Simpson, 1945).[4]

---

[4] In evaluating these and similar figures one must bear in mind that comparing

19 To establish accurately the number of extant species in an order is difficult because of our poor understanding of the taxonomy of species. Probably they number about 150 (according to Haltenorth and Trenze, 1956). Thus they number more than all the remaining ungulates taken together and comprise about 4.3% of all mammalian species. On the average each genus contains 1.6 species and every family about 17. The largest number and diversity of species is seen in Africa (72 species) and Asia (65 species); the corresponding figures for North America, South America, and Europe are 12, 15, and 11 species.

In most parts of the world wild artiodactyls are of definite and sometimes great economic importance as game animals, providing meat, hide, and other products for making consumer goods, and raw material for pharmaceutical preparations. They are valued everywhere as sport objects. Many species have greatly reduced in numbers and their range has shrunk; other have been totally destroyed; and several are now under total or partial protection. Artiodactyls are one of the important animal groups protected under conservation programs in nature preserves throughout the world. Some species have been acclimatized while others serve as controlled game animals.

Some artiodactyls are responsible for the spread of diseases, including protozoans (trypanosomiasis), among man and domestic animals. Consequently they are destroyed in some areas (tropical Africa). Together with perissodactyls they include the most important domesticated animals. Some species are both wild and domesticated or semidomesticated.

Artiodactyl fauna of the Soviet Union comprise (excluding domesticated animals and fallow deer) a total of 19 species, about 1.5% of the species of the order and about 6.3% of the mammalian species in Soviet Union. Two of the 3 suborders are represented (the third, Tylopoda, is present in a domesticated state), two of the 4 infraorders, three of the 6 superfamilies, three of the 9 families, seven of the 15 subfamilies, and fourteen of the 86 genera. Artiodactyls thus constitute the most abundant group of ungulates in the Soviet Union.

Artiodactyls are found throughout the Soviet Union but the number of species in the south is greater. The distribution of almost

---

extinct and extant forms is, strictly speaking, not entirely logical since the very brief period of existence of extant forms in the evolution of groups is thus compared with the entire historic period. Precisely for the same reason placing extant and extinct forms together in a common taxonomic system should, at best, be tentative.

all species underwent significant changes and shrank in the last century; some even became totally extinct or virtually so. In recent years the ranges of some species have been artificially expanded by acclimatization.

Artiodactyls are found in the Soviet Union in all topographic zones and at altitudes exceeding 5,000 m above sea level. Most species are stenotopic (some strictly) and a few eurytopic. Some are typical gregarious forms while others live in small groups or even singly. In many species the herd instinct varies intensely throughout the course of a year. Some undertake significant seasonal migrations, while other species are stationary or shift only insignificantly in altitude.

Nearly all these animals are distinctly polygamous. Mating usually occurs in autumn and the young are born in spring. Some species possess a latent stage of development of the fertilized egg. Offspring generally number no more than two but sometimes reach 10 or 12. Except for one, Soviet species are herbivorous. One or two molts occur each year. Seasonal variability is evident in several species, sexual dimorphism prominent in most, and age-related changes seen in some.

In the Soviet Union artiodactyls play an important role in the hunting trade. They provide meat and hide and some yield fur and raw material for pharmaceutical and perfume industries and other consumer goods. Some products are exported and in some places play a vital role in the local economy. Some are maintained in a semidomesticated state; measures have been undertaken for the domestication of several.

During the last century most species of artiodactyls underwent intense numerical reduction; some have since been placed under total or partial protection. In recent years the population of some species has risen and their range been enlarged as a result of such conservation measures. Artiodactyls represent an important group protected by conservation laws in most preserves. (V.H.)

20 *Key to Suborders and Families of Artiodactyla*

1 (4). Incisors present on upper jaw.

2 (3). One pair of incisors present on upper jaw. Enlarged nails present in place of normal hooves; only two digits on legs (lateral ones absent). One or two fatty humps present on back. Domesticated animals .... Suborder **TYLOPODA,** Camel Family, **Camelidae.**

3 (2). Three pairs of incisors on upper jaw. Normal hooves present;

four digits on legs (small lateral ones present). General appearance of swine .... Suborder **SUIFORMES**, Pig Family, **Suidae.**

4 (1). Incisors absent on upper jaw .... Suborder **RUMINANTIA.**

5 (6). Nostrils wide-set; distance between them more than shortest distance from lower tip of nostrils to edge of lip. Sometimes light-colored spots present on skin. Horns, if present, in the form of hard bony rods or covered with skin with short hair ("velvet"), and usually branched (main beam with lateral tines). Teeth with relatively low crowns and vertical ridges and furrows on lateral surface do not reach edge of alveolus; ridges merge into horizontal ridge at base of crown (Fig. 2). Upper canines often present. Between frontal, nasal, lacrimal, and maxilla large, irregularly triangular vacuity present on each side .... Deer Family, **Cervidae.**

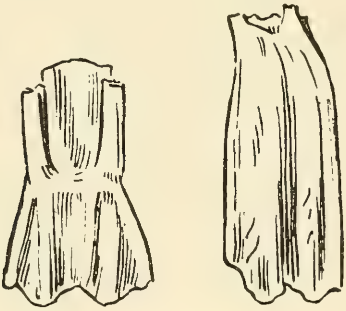


Fig. 2. Left—Upper molar of deer (*Cervus,* family Cervidae); brachyodont with transverse ridge connecting outer ridges of crown at its base. Right—Same of goat (*Capra,* family Bovidae); hypsodont without transverse ridge (from Sokolov, 1959).

6 (5). Nostrils close-set; distance between their inner edges less than distance from lower end of nostril to lower edge of lip.[5] Bright spots absent on skin. Horns, if present, in the form of horny sheath covering bony axis in the form of an out-growth of frontal bone and unbranched (main beam with no lateral tines). Teeth with relatively high crowns and vertical ridges and furrows on lateral surface reach edge of alveolus; horizontal ridge at base of crown absent. Upper canines absent. Between frontal, nasal, lacrimal, and maxilla vacuity absent or, if present, small and slitlike... Cattle Family, **Bovidae.** (V.H.)

[5] Ratio differs in European wisents and domesticated yaks.

Suborder SUIFORMES Jaeckel, 1911

21 Artiodactyls are sometimes generalized but often specialized small-, medium-, or large-sized animals. In Suiformes the general build is massive and bulky, the limbs short, and the trunk massive and heavy.

The number of digits is usually four; a few have three digits on the hind limbs.

Reduction of the lateral digits is relatively poor; in some they differ morphologically and functionally only slightly from the medial and reach to the ground. All metatarsal and metacarpal bones fully developed and normally joined with tarsal and carpal regions. Fusion of metatarsal and metacarpal bones nonexistent or only rudimentary. Cannon bone absent. Terminal phalanges of digits covered with hooves. Ulna and (with many exceptions) fibula normally developed and free.

Elongated facial part of skull usually wedge-shaped; in some, extended facial part greatly enlarged anteriorly. Longitudinal axis of skull more or less straight. Orbit opens posteriorly (with one exception). Ethmoid pit absent. Sagittal crest present. Horns absent. Mastoid bone covered. Articular condyle of lower jaw longitudinal.

Canines invariably present and usually very well developed. Upper incisors usually number three and occasionally two or one. Molars bunodont or brachyodont, and exceptionally hypsodont.

Stomach relatively simple and consists of not more than three sections. Suiformes are nonruminants. Cecum medium in size and simple or else absent. Sweat glands usually absent, present exceptionally. Hair coat in some animals greatly reduced and bristly in most. Teats inguinal, or inguinal and abdominal, numbering one to six pairs. Placenta diffuse. Sexual dimorphism either not manifested or poorly so. Age-related changes generally absent.

Suiformes are relatively slow-moving animals incapable of swift or long-distance running. Two major biological types are known: swine and hippopotami. They inhabit tropical to temperate forests, wooded zones of mountains, steppes, and marshy and fluvial regions. Most prefer extremely humid regions and one genus leads an amphibious life (*Hippopotamus*).[1] They do not form significant herds and live in small groups, rarely singly. Offspring number one

---

[1] The pygmy hippopotamus (*Choeropsis*), in spite of common opinion, differs greatly in its mode of life from the common hippopotamus.

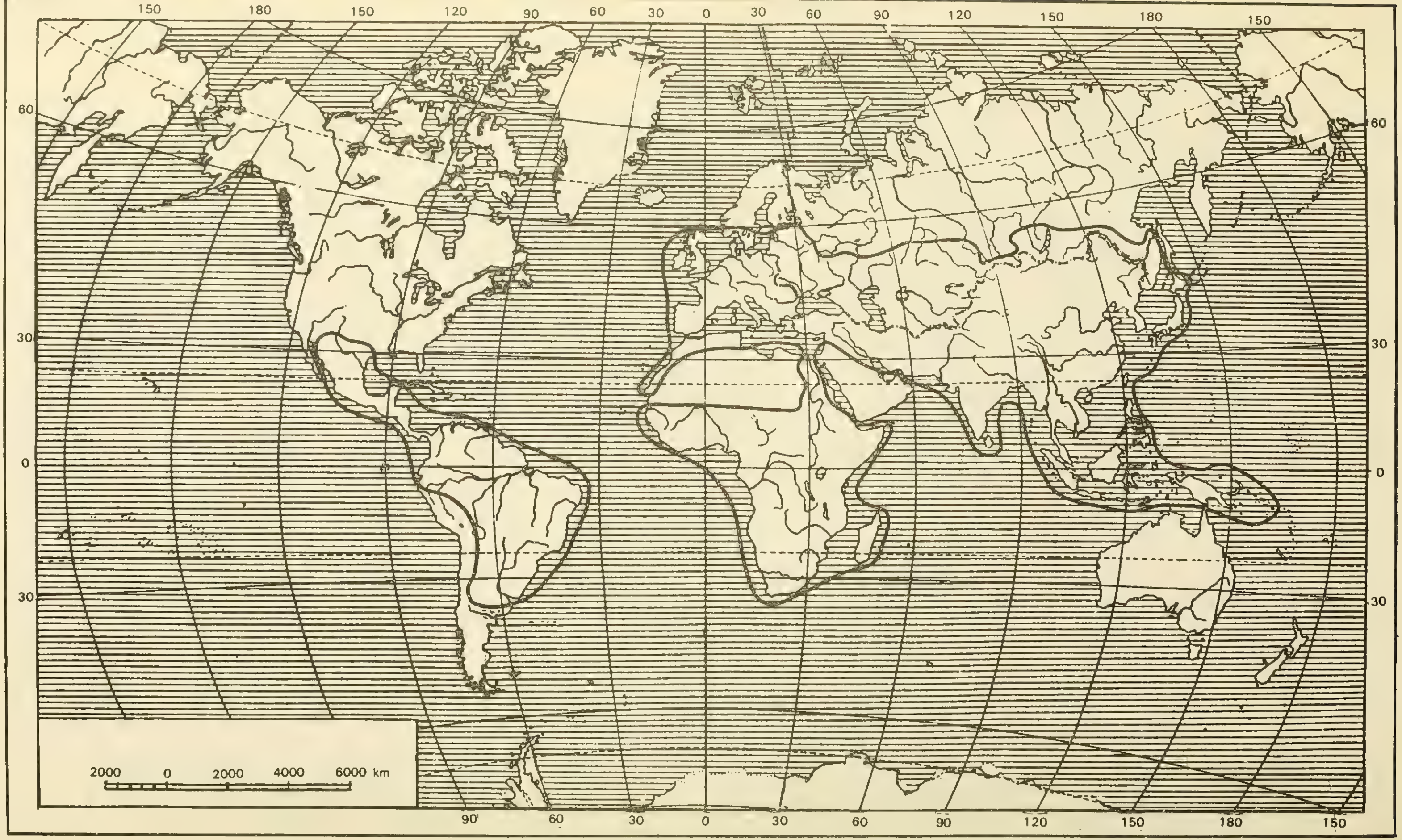

150
180
150
120
90
60
30
0
30
60
90
120
150
180
150
60
30
0
30
2000
0
2000
4000
6000 km
90
60
30
0
30
60
90
120
150
180
150

Fig. 3. Geographic range of nonruminant artiodactyls (scale in km). New World—pecarry (Family Tayassuidae) and Old World—hog (Family Suidae). Reconstructed range. V.G. Heptner.

rarely, two occasionally, and generally ten to twelve.

23 Most Suiformes are omnivorous with a predominantly herbivorous diet; some are purely herbivorous and feed mainly on aquatic vegetation.

These nonruminants are widely distributed and occur in central and southern Europe and Asia, in the south up to the extreme points of habitat of the order, and in the north up to the southern part of the Scandinavian Peninsula and Gulf of Finland, Oka [River], southern Urals, southwestern Siberia, Altai [Mts.], Sayan [Mts.], northern extremity of [Lake] Baikal, and the lower Amur [River].* They are also found in North America in the north up to southwestern Texas, southeastern New Mexico, and southern Arizona. In Central and South America they occur in the south up to the equator, northern and northwestern Peru, Uruguay, and northern and central Argentina (up to the latitude of La Plata [River] and slightly southward). In Africa, they are found in northwest Africa, the Nile basin, and throughout the continent south of the Sahara, in Madagascar, and only in the northwestern Mediterranean Sea portion of the Arabian Peninsula (reconstructed range).

Recent nonruminants differ distinctly from all other artiodactyls and there are no intermediate forms whatsoever between the various recent suborders. Morphologically, and partly biologically (omnivorous feeding), the suborder of nonruminants, in spite of the high degree of specialization of some of its members, can be considered relatively poorly specialized and primitive. Forms at the commencement and in the first half of the Tertiary period point to a close phylogenetic relationship between nonruminants and the rest of the artiodactyl suborders. Keeping in view the infraorder Palaeodonta, some scientists regard nonruminants as the ancestral group giving rise to all other recent as well as extinct groups of artiodactyls.

Members of the nonruminant suborder are already known from the Lower Eocene of America and Europe. They belong to the extinct infraorder Palaeodonta. Recent groups appeared not earlier than the Middle Eocene or Lower Oligocene (Europe). In the Tertiary period nonruminants developed relatively more abundantly than in the recent epoch. In the Eocene and Oligocene epochs they predominated, later giving rise to ruminants. At present they represent a naturally declining group although there are some flourishing species among them.

---

*The style of the Russian original often omits descriptive nouns from place-names; the reader should bear this in mind—Sci. Ed.

The suborder is divided into two* infraorders of which two are extinct (Palaeodonta and Oreodonta) and two extant (Suina and Ancodonta). Suina include one superfamily—Suoidea—with two families; Suidae—true hogs, and Tayassuidae—peccaries or New World hogs. The latter family consists of one (according to some, two) genus (*Tayassu*) with two species and is confined to America. These are unique nonruminants of the New World. There are no extinct families among Suina.

Ancodonta include one extinct and one recent superfamily. The latter, Anthracotherioidea, consists of three families, of which only one is recent, i.e., Hippopotamidae. It consists of two monotypic genera—*Hippopotamus* and *Choeropsis* (pygmy hippopotamus)—distributed in equatorial Africa.

The suborder consists of 134 genera (about 32%) of all artiodactyls) included in 8 families (about 32%). Of these, eight genera (about 9.3% of recent artiodactyls), included in three families (12%), are extant.

The taxonomy of species of the suborder is simple. The total number of extant species is 12. Most (six) belong to Africa, two to America, three to Eurasia, and one is Eurasio-African.

These are game animals providing meat, hide, and other material for making consumer goods ("ivory bone," hippopotamus teeth) and are essentially objects of sport. At some places they cause significant damage to plantations. One species is highly domesticated.

Fauna of the Soviet Union include one of the two infraorders (Suina Gray, 1868), one of the two superfamilies (Suoidea Cope, 1887), and one of the three families (Suidae Gray, 1821). One species occurs in the Soviet Union (about 8% of the species of the suborder) representing 0.3% of the mammalian species of this country.

Suiformes are distributed in the southern half of the Soviet Union.

---

*Misprint in Russian original; should read four—General Editor.

Infraorder SUINA Gray, 1868

24 Family SUIDAE Gray, 1821 (Swine)

Suidae are nonruminants of medium size.

All limbs with four digits each. Lateral digits well developed but distinctly shorter than medial ones, usually do not reach the ground, do not have a normal joint with the tarsal and carpal regions, and are markedly turned backward. Ulna and fibula free.

As a result of elongation of mainly the maxillae and partly the premaxillae, skull elongated and wedge-shaped and not broadened anteriorly. Frontals, parietals, and supraoccipitals pneumatic. Orbit open. Facial part of lacrimal well developed and separates jugal from frontal or even frontal from maxilla. Usually two lacrimal foramina present. Hard palate elongated and extends backward beyond posterior edge of tooth row. Tympanic bulla swollen, pyriform, and divided by bony septa into innumerable tiny chambers. Exoccipital and squamosal fused and mastoid set deep inside and not visible from the surface (covered). Dental formula (in the type): $i\frac{3}{3}$, $c\frac{1}{1}$, $pm\frac{4}{4}$, $m\frac{3}{3}$, but a reduction in number of incisors (to $\frac{1}{3}$) and premolars (to $\frac{2}{2}$) occurs in different genera. Canines grow throughout life and upper ones turned upward. Incisors, premolars, and molars elongated posteriorly and typically bunodont and brachyodont; hypsodont molars and horizontal succession of teeth exceptional.

Anterior end of snout extends into a small, relatively poorly mobile proboscis with a vertically slit anterior surface on which the nostrils open directly. Proboscis has a cartilaginous base which usually ossifies (os nasi). Teats abdominal or inguinal and abdominal and number more than two pairs. Cecum present. Stomach simple, with only a small supplementary diverticulum ventriculi. Sexual dimorphism relatively poor. Age-related changes seen in some.

Biologically Suidae are fairly monotypic, living in forests of different types, in forest steppes and steppes, in the plains, and at moderate altitudes on mountains. They exhibit a preference for highly humid regions. Offspring number 4 to 6 and sometimes more (up to 10, and probably even 12). The animals are omnivorous with a predominantly herbivorous diet.

25 The distribution of Suidae extends over part of the range of the suborder falling in the Old World.

Extant hogs represent a fairly monotypic, taxonomically well-defined group. They differ notably from hippopotami (different infraorder) but are highly similar to peccaries (family Tayassuidae). Sometimes both groups are merged into a common family with the rank of subfamilies. In reality the two groups are quite distinct (almost totally rudimentary fourth digit on the hind limb which is functionally tridactyl, fusion of proximal part of metapodia III and IV, special articulation of lower jaw, dorsal gland, etc. found in Tayassuidae). The two families are distinct even in the lower Tertiary. Peccaries are seen from the Lower Oligocene onwards and have developed independently in the New World where true hogs (Suidae) are absent and, in fact, were never present.[2] Among nonruminants true hogs represent an extremely primitive group, closest to the ancestral types of the infraorder Suina. Nevertheless, Tayassuidae are characterized by several primitive features, even more primitive than those of Suidae.

Representatives of these families, belonging to extinct subfamilies, are known from the Lower Oligocene of Europe. The extant subfamily Suinae is seen from the Lower Pliocene onwards in Europe and Asia.

Family Suidae is subdivided into five subfamilies, of which four are extinct (some survived up to the Pleistocene) and one extant, i.e., Suidae.* The family comprises 22 genera (about 16% of all nonruminants) divided among five subfamilies (out of 19, i.e., 26%). Extant genera in the family number five out of eight in the suborder (62%): *Sus*—Eurasia, *Potamochoerus, Hylochoerus, Phacochoerus*—Africa, and *Babyrousa*—Sulawesi (Celebes).

The total number of extant species in the family is eight, i.e., 66% of the extant species of the suborder or about 4% of the number of extant species of the order and about 0.3% of all extant mammals.

Only one genus is known in the Soviet Union (20% of extant forms). (V.H.)

I. BOAR, OR WILD SWINE

Genus *Sus* Linnaeus, 1758

1758. *Sus* Linnaeus. *Syst. Naturae,* 10th ed., vol. 1, p. 49. *Sus scrofa* Linnaeus.

---

[2] Tayassuidae were present in Europe and Asia, continuing in Asia up to the Lower Pliocene.

*Error in Russian original; should read "Suinae"—General Editor.

Occipital region of skull highly raised and posterior profile vertical or slanted forward. Exostoses on skull and at base of upper canines absent or latter very poorly formed.

Dental formula: i $\frac{3}{3}$, c $\frac{1}{1}$, pm $\frac{4}{4}$, m $\frac{3}{3} = 44$. Premolar $\frac{1}{\ }$ has no milk precursor and, like i $\frac{3}{\ }$ (even i $\frac{\ }{3}$), tends to disappear (often absent in old animals). Medial incisors much larger than outer; lower incisors large and set almost horizontally. Canines grow throughout life; lower ones trifaceted. Canines distinctly smaller in females than in males. Tips of upper canines beveled due to grinding against lower ones. Molars brachyodont with relatively sharp cusps; succession of molars normal.

Hair coat well developed, bristly in some and soft, furry in others; on neck and along spine hair long and sometimes very thick forming a prominent "mane".

Teats six (*Sus*) or three (*Porcula*) pairs and abdominal and inguinal.

Adults uniformly colored (sometimes with light-colored mark on snout). Young of most species with longitudinal light-colored patches on body.

Habitats—forests, tugais [vegetation-covered bottomlands], and reed thickets.

The geographic distribution of genus *Sus* (reconstructed) covers northwest Africa and Rio de Oro, Egyptian region of United Arab Republic, and Sudan (Sennar, Kordofan, and adjoining territories).
26 In Eurasia the genus is found in the north in southern Sweden, Gulf of Finland, Oka, southern Urals, southwestern Siberia, and northern Baikal and Amur; in the south in Asia Minor, western Mediterranean, parts of Arabian Peninsula (Syrian region of United Arab Republic and Palestine), Ceylon, Nicobar and Andaman Islands, Sumatra, Java, Sumbawa, Sumba, Rota, Timor, Ara, Kai, New Guinea, Louisiade, Solomon Islands, Bismarck and Admiralty Islands, some small islands on the northern coast of New Guinea (Yapen, for example), Waiges, Moluccas, and Philippine Islands. Hainan, Taiwan, and the islands of Japan,[3] including Ryukyu, also fall within the range of *Sus*.

---

[3] The natural geographic range of the genus in the extreme southeast is very difficult to demarcate, in fact, almost impossible. In the distant past local inhabitants of the islands, who were excellent sea-farers, imported domestic pigs (rather unique as domestic animals) which ran wild and now represent current wild forms. This is primarily true of New Guinea and the adjoining island groups occupied by *S. papuensis*. However, wild pigs exhibit signs of domestication in certain other areas of the islands between Australia and Asia, even for example Sulawesi (Celebes) (the entire group of *celebensis* type). Evidently in some places hybridization of truly wild

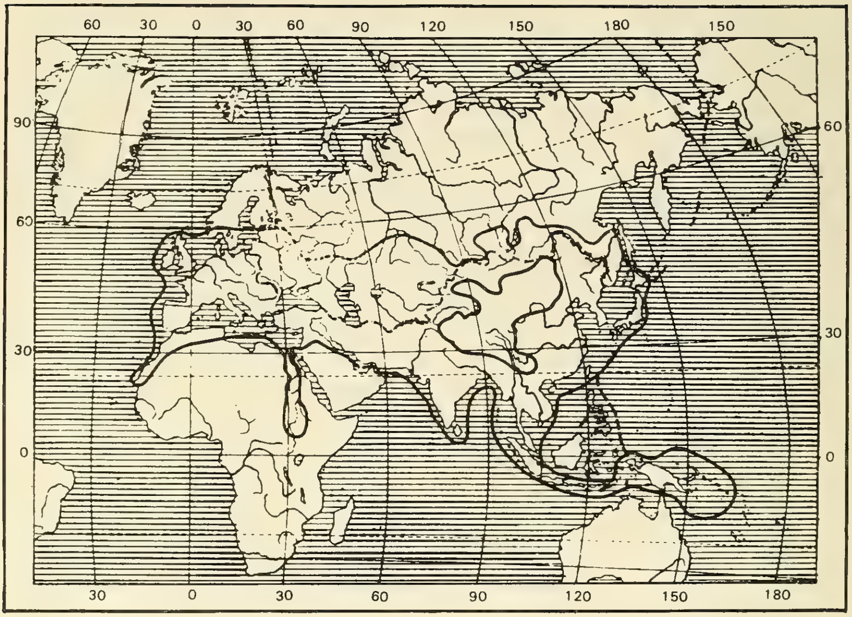


Fig. 4. Geographic distribution of extant wild boars, genus *Sus* L. (reconstructed).

Gap occurs in range in central parts of Asia. Continuous line demarcates geographic range of common wild boar (*Sus scrofa* L.). Broken line separates that part of range where only *Sus barbatus* occurs. On some islands and in Malacca both *Sus scrofa* and *Sus barbatus* are found. V.G. Heptner.

Genus *Sus* is distinctly separate from other genera of the family. It is closely related (through *S. barbatus*) to genus *Potamochoerus* (Africa, Madagascar). Genus *Sus* represents the least specialized group of recent hogs and is close to primitive types of the family; it is known from the Lower Pliocene of Europe and Asia.

Genus *Sus* is very compact and contains so few species that attempts to divide it into several subgenera (*Euhys, Aulacochoerus,* and *Dasychoerus*) are unfounded. Only the separation of subgenus *Porcula* with one species (*S. salvanius* Hodgs.) appears justifiable.

The taxonomy of species of genus *Sus,* unlike that of other genera, was extremely confusing until very recently. Seven, eight, and even more species with a large number of subspecies were acknowledged 27 in the genus. Particular difficulties were posed by forms from South Asia, mainly the island region between Asia and Australia.

indigenous local hogs with the imported forms which ran wild occurred. It is highly possible that the true geographic range did not extend so far southeast as shown here.

Apart from other reasons (incomplete descriptions and the like), complexity of development of structures in these forms made classification difficult. In addition to phenomena associated with island life, a powerful influence has been exerted by hybridization of domestic and wild forms and the transformation of the former into the latter.

In recent years the situation has been clarified somewhat and only three species should properly be placed in genus *Sus*: *S. scrofa* (including the complex of *S. leucomystax* from east Asia, *S. cristatus* from India and Indochina, *S. vittatus* from Sumatra and Malacca, and some others), *S. barbatus* (including *verrucosus, celebensis,* and some others) from Malacca, Sumatra, Java, Kalimantan (Borneo), Sulawesi (Celebes), Moluccas and Philippine Islands, and *S. salvanius,* the pygmy hog from Sikkim, Nepal and Bhutan.[4]

Genus *Sus* thus includes about 25% of the species of the family.

Only one species is known in the Soviet Union (33% of extant species of the genus), representing 0.3% of the mammalian species of the Soviet Union. (V.H.)

1. ***Sus* (*Sus*) *scrofa*** Linnaeus, 1758[5]

1758. *Sus scrofa.* Linnaeus. *Syst. Naturae,* 10th ed., vol. 1, p. 49. Germany. 1811. *Sus europaeus.* Pallas. *Zoographia Rosso-Asiatica,* vol. 1, p. 265. Caucasus to Baikal, substitute for *Sus scrofa* Linn. 1875. *Sus scrofa* var. *nigripes.* Blandford. *Journ. As. Soc. Bengal,* vol. 44, pt. 2, p. 112. Tien-Shan in Kashgar. 1888. *Sus ussuricus.* Heude. *Mèm. conc. l'Hist. Nat. Emp. Chin.,* vol. 2, p. 54. Ussuri valley. 1889. *Sus leucomystax* var. *continentalis.* Nehring. *Sitzungsber. Ges. naturf. Freunde, Berlin,* p. 141. Vladivostok. 1892. *Sus gigas.* Heude. *Mèm. conc. l'Hist. Nat. Emp. Chin.,* vol. 3, p. 191. Vladivostok. 1912. *Sus attila.* Thomas. *Proc. Zool. Soc. London,* p. 183. Kolozvar (Klausenburg, now Cluj) in Transylvania (Rumania). 1918. *Sus falz-feini.* Matschie. *Sitzungsber. Ges. naturf. Freunde, Ber-*

---

[4] This species (height at shoulders about 30 cm and skull length 150 to 160 mm), described as early as 1847, was long regarded as non-existent and merely a name used to describe young or abnormal or underdeveloped animals. The independent existence of this species was demonstrated only recently (Ellerman and Morrison-Scott, 1951).

The enigmatic form *S. gargantua,* a gigantic hog of Borneo known only from a single skull, is not included here.

[5] Young animals, up to one year of age, irrespective of sex termed "sucklings", and from one to two years "juveniles". Adult males called "boars". Fully grown adults with good canines (tusks) called "tuskers" and old males with tusks "loners". Adult females called "sows".

lin, no. 8, p. 1. Naliboki, about 75 km west of Minsk. 1922. *Sus leucomystax sibiricus.* Staffe. *Arb. d. Lehrkanz. Tierzucht. a.d. Hochschule f. Bodenkultur, Wien,* vol. 1, pp. 51–58, Pls. I–III. Tunkin mountain range, southern Siberia. 1930. *Sus scrofa raddeanus.* Adlerberg. *Doklady Akad. Nauk USSR,* p. 95. Sugu-nor, southern Hentei, Mongolia. (V.H.)

Diagnosis

Sus (*Sus*) *scrofa* is the only species of genus *Sus* found in the Soviet Union.

Description

General build massive and bulky with short and relatively thin legs. 28 Trunk relatively short with an extremely massive anterior part and poorly developed posterior part. Back in region of shoulder blades highly raised (humped) and neck thick, short, and nearly immobile. Head very large and constitutes about one-third body length (including head); projects forward like a wedge and continues inconspicuously into neck and withers. Tail thin and short, not reaching hock, with a few elongated hairs at tip.

Ears long and broad. Eyes small and deep-set. Snout projects; nostrils set directly forward, open on broadened, blunt edge of snout. Upper and lower canines protrude from mouth of adult males.

Hooves of medial digits larger and elongated, with pointed tips and edges bent downward, capable of quick movement; hooves of lateral digits also well developed, set low, and relatively large, long, and sharp.[6]

In general appearance females somewhat lighter in build and more slender than males, with a smaller hump and less massive anterior trunk portion.

In winter wild boar are covered with long, dense, resilient, somewhat curly bristles underlaid with an extremely short, dense lining of fur consisting of thin, curly, soft, downy, light brown or brown-colored hair. The base of each bristle is dark-colored (black or blackish-brown) and the terminal part lighter. The bristles on the head are short, longer on the sides, especially on the back, and long-

---

[6] Compared to other Russian ungulates the lateral digits and their skeleton are less reduced and more functional in wild boar. The metapodium represents a compact, greatly perfected supporting system, especially when moving on soft ground. When resting on all four digits, the weight load on 1 cm^2 is roughly reduced by 1.5 times, i.e., from 500 to 320 to 390 g (Sludskii, 1956).

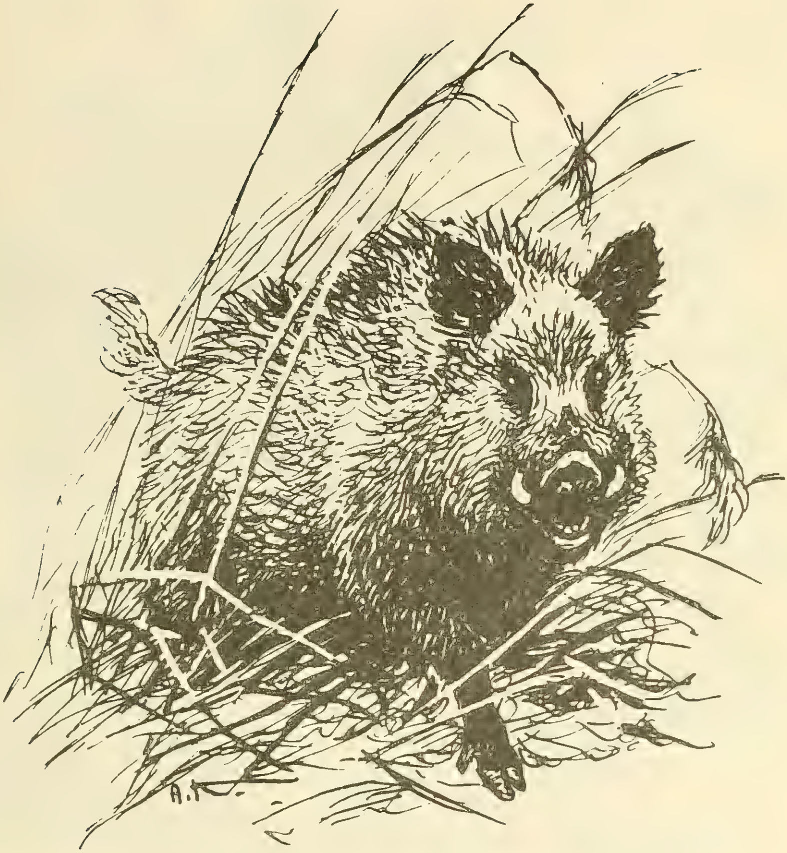


Fig. 5. Tusker. Sketch by A.N. Komarov.

est in the middle of the back in the anterior part of the body. A 29 characteristic crest forms here and on excitation these bristles stand erect. Both the abdomen and legs are covered with very short bristles. The latter are directed forward on the rear of the abdomen and in the lower part of the neck, and directed backward on the rest of the body.

The overall color of the animal depends on the hue of the hair (bristle) tips and is highly variable. Wild boars in Balkhash vary from light brown to pale yellow (sandy) or even white. In Belorussia rusty-brown-colored animals, lighter-colored animals, and even totally black ones are seen. In Ussuri region ocherous, light brown, and black individuals are found. Extremely light-colored animals have the silver-gray color of badgers. In a new coat individual body parts vary in color as follows: posterior part of head, neck, back,

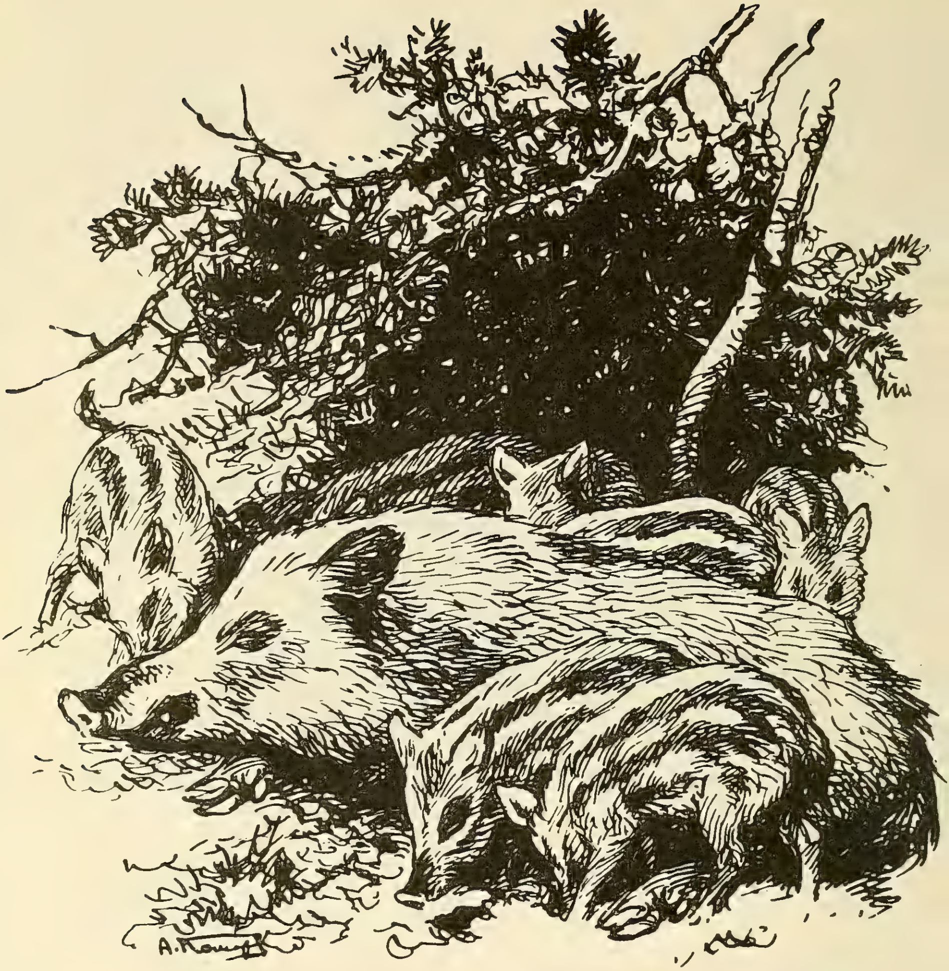


Fig. 6. Sow with sucklings. Sketch by A.N. Komarov.

sides, and tail relatively light and anterior parts like the snout and ears, in addition to the legs dark, sometimes black. In some forms (see below) a light-colored patch runs from the corner of the mouth backward. Hooves are always black.

By spring the hair cover, especially in central Asia and Kazakhstan, has usually undergone intense fading and the color particularly of sucklings and juveniles is notably lighter. In summer, when the winter hair is shed and the new coat has just begun to grow (one molt occurs in wild boar, see below) and the fur lining has not yet formed, wild boar appear very dark, often dark brown and black, or black. This is mainly because the black skin shows through the sparse hair coat. Hooves and snout are black. There are no sex-related variations in color.

30 Color varies sharply with age, however. Sucklings retain the relatively soft juvenile hair with which they are born and their general color is light brown or rusty-brown. Longitudinal, light-colored, pale yellow bands extend along the sides and back. The adult coat develops in the fourth month after birth. Juveniles, at least in some areas, are usually more lightly colored than adults and older individuals.

Some geographic variability is also evident, in addition to distinct individual variations of pigmentation (see below).

The skull of the male wild boar is massive and characterized by great development of upper and lower canines which grow throughout life. The upper ones are massive with a blunt apex and edges, relatively short, triangular in cross section, initially grow sideways and later curve upward; in older animals they are turned backward. The lower canines are also triangular in cross section but much longer (their exposed part is 10 to 12 cm or more long[7]), turned back like a saber, with sharp cutting edges and a very sharp apex. A prominent growth along the edge of the jawbone occurs in the basal region of the upper canines.

Canines begin to grow in the male even in the first year of life and are well developed by the age of three years; they continue to grow throughout life but are somewhat flexed backward in later years, especially the upper ones. Canines are poorly developed in the female and do not serve as tools; they are of little importance in burrowing, rooting, and so on.

Sequential changes linked with age are distinct in the skull with advancing age; the relatively short facial region of the young becomes greatly elongated.

In August, before the breeding period, a "stuffing" (also called "fat" or "armor") of subcutaneous tissue resembling cartilage forms along the sides of the body of the male and protects him during fights. This tissue covers the shoulder blade region and extends backward to the last rib; it is thickest (2 or 3 cm) in the region of the shoulder blades and gradually thins backward toward the rump and forward toward the neck. Dorsal to the preputial orifice a special sac the size of a large egg when extended or even slightly larger (diverticulum preputiale) also occurs in the male. Some urine collects and settles in it giving off a sharp, unpleasant odor. The function of this diverticulum and its characteristic musculature is not entirely understood; it evidently has a mechanical function and helps prevent the outflow of blood from the corpus cavernosum.[8] Hesse's cardiac index is very low—4.4 to 6.5 (Bannikov, 1955).

---

[7] Some record specimens of canines are much longer—24 or 25 cm along the outer curvature including the portion embedded in the bone. A large lower canine has a nearly regular semicircular form when removed from the socket.

Wild boar vary considerably in size in accordance with age. They grow slowly, attaining full growth at the age of five or six years; even then growth does not cease. Sex-related differences are also notable; females are invariably smaller than males. Weight also changes, depending largely on the degree of feeding during different years and seasons. During the breeding season males become highly emaciated. Size and weight also reflect some geographic variability.

The size of adult boars (not younger than five to six years) from the lower reaches of the Ili (Semirech'e) is as follows (in cm)[9]: body length: males 148 to 174 (M* 160) (n=11), females 127 to 157 (M 144) (n = 12); length of torso: males 90 to 118 (M 98) (n = 11), females 80 to 108 (M 90) (n = 9); height at withers: males 79 to 102 (M 86) (n = 11), females 80 to 86 (M 77) (n = 12); height at rump: males 78 to 102 (M 31 80) (n = 11), females 70 to 81 (M 74) (n = 10); tail length: males 20 to 29 (M 24.5) (n = 11), females 19 to 26 (M 22) (n = 10); length of ears: males 13 to 16 (M 14) (n = 11), females 12 to 14 (M 13) (n = 11); chest circumference: male 113 (n = 1) and female 95 (n = 1) (Sludskii, 1956). The average body length of western (European) wild boar is about 150 cm and height at withers about a meter.[10]

The weight of Latvian wild boar may reach 200 or even 236 kg (Kalnin'sh, 1950) and of Belorussian animals 256 kg, although boar usually weigh about 150 kg or slightly more (Serzhanin, 1955). Carpathian animals weigh 120 to 180 kg and exceptionally up to 250 (Tatarinov, 1956). Wild boar in the Caucasian preserve in the 1930's weighed as follows: males 64 to 178 kg (M = 166 kg) and females 48 to

---

[8] In any case it is not a musk gland as reported by some authors (Sludskii, 1956).

[9] The measurements given for Semirech'e wild boar are far from maximum values. Evidently they often reach as much as 200 cm in length. At the same time references to body lengths of 230 and 240 cm and height at withers of 110 cm or more, especially of western animals (Latvia and Belorussia; Serzhanin, 1956; Kalnin'sh, 1950) are dubious or relate only to exceptional specimens.

*Here and elsewhere "M" stands for mean measurements—General Editor.

[10] Footnote indicated but none given in Russian original—General Editor.

108 kg (M = 68 kg) (Donaurov and Teplov, 1938); early in this century old males weighed 240 to 255 kg and females 120 to 145 kg (Dinnik, 1919). Animals of the Astrakhan' preserve (Volga delta) in the 1930's weighed up to 250 to 260 kg (males; Lavrovskii, 1952) and wild boar in Syr-Darya up to 240 kg. A few years earlier animals of 270 kg and even 320 kg were reportedly caught. Wild boar of Ili touch the scale at 220 to 240 kg and sows at 95 to 100 kg (Sludskii, 1955). In Eastern Siberia wild boar attain weights of 240 or even 272 kg. Boars of the Far East are particularly heavy; old tuskers tip the scales at 300 to 320 kg (Abramov, 1956).

As can be seen from the data available, the Caucasus wild boar used to be larger than they are at present. The weight of animals from the northern Caspian coast in the middle of the last century went up to 320 kg. Reduction in size of wild boar has been reported nearly everywhere in the world; 200 pood* animals are now rare even in the Far East where boar weighing 200 kg are now considered large. This is the result of thoughtless hunting, due to which the average age of the animals is lowered since they are not allowed to grow to maximum size. It is significant that in the Astrakhan' preserve in the 1940's the animals were notably larger than at the end of the last century when they were numerically very abundant. At that time they attained a maximum weight of only 192 kg versus 250 to 270 kg at present (Sludskii, 1956).[11]

In Semirech'e the live weight of sucklings at the age of 8 to 11 months is 21 to 30 kg for males and 20 to 29 kg for females, i.e., at the time of completing their first year suckling weight is about one-fourth the adult weight. Their body length at that time is 93 to 115 cm in males and 92 to 105 cm in females. Young pig between the first and second year of life weigh 25 to 54 kg and 35 to 44 kg (male and female respectively); this represents roughly one-half or slightly less than the average weight of adult animals of corresponding sexes. The body length is 120 to 130 cm and 100 to 120 cm (male and female respectively) (Sludskii, 1956). Newborns weigh 1,620 and 1,360 g respectively (Ussuri region; G.F. Bromlei). (V.H.)

Taxonomy

Within the genus *S. scrofa* is closest to bearded swine (*S. barbatus* Müll.) inhabiting Malacca and other islands (see Fig. 4 and description of geographic range of wild boar). The third species of the genus—*S. salvanius*—found in a very narrow region in the Himalayas and possibly a relict form, stands quite isolated and is usually placed in a separate subgenus or sometimes even a separate genus, *Porcula*. (V.H.)

---

*Pood = 16.38 kg—General Editor.

[11] Mean weight of male from Central Europe 130 kg; maximum evidently about 230 kg.

Geographic Distribution

The geographic distribution extends in Europe up to 60 to 55° N lat; in Asia up to 55 to 50° N lat. and in the south includes India and Ceylon and a significant part of the island zone from Malacca to Solomon Islands, and northeastern and northwestern Africa.

Geographic Range in the Soviet Union

The range in the Soviet Union covers the extreme northern section of the range of the species. It extends over the southern half of the European part of the country, the Caucasus, and the southern fringes of the Asiatic part of the USSR.

32 The range of wild boar in the Soviet Union has varied significantly over the years. This can be seen from the fact that almost the entire northern fringe of the range falls within the Soviet Union and that the species has survived in very large expanses under minimal or close to minimal climatic (temperature and snow) and trophic conditions. Under such conditions the lability of the fringe of the range and its boundaries is readily apparent. The human factor has also played a major role in changing the range of modern boar. Foremost among the various causes are hunting the animals and destruction of their biotopes. Against the background of minimal conditions such factors become acute. It is very easy to eliminate wild boar populations and very difficult to restore them.

In the last century the range of wild boar shrank extensively in the European part of the USSR. The animal disappeared almost throughout the territory except in the far west and in a negligible section in the southeast (see below). In the region from the Ural River to the Altai also the boundary has fluctuated extensively and shifted far to the south. A particularly intense destruction of animals and reduction of range occurred in the second half of the nineteenth century and in the first few decades of the twentieth.[12] The range was reduced to its minimum evidently in the 1930's.

[12] It is possible that the process was somewhat different in the Baltic region and the second half of the nineteenth and the beginning of the twentieth centuries represent a period of expansion of the range in the north (Ling, 1955).

A noticeable expansion of the range of wild boar commenced in the 1930's in the European part of the Soviet Union and western Altai. Expansion proceeded very rapidly between 1940 and 1960, expecially in Kazakhstan. However, in other regions, for example northern Caucasus, range expansion toward the north was not seen. By the mid-1950's the range boundary had advanced significantly but extended no farther since adequate numbers could not be formed in the newly occupied territories. In many places permanent habitation is still not seen and wild boar is an intruder. The process of colonization of new territories is still going on. Further expansion depends on climatic conditions in future years and, most important, on human activity. It is significant that under the present conditions of establishment of wild boar the boundaries have reached their former maximum limits in the north in several places.

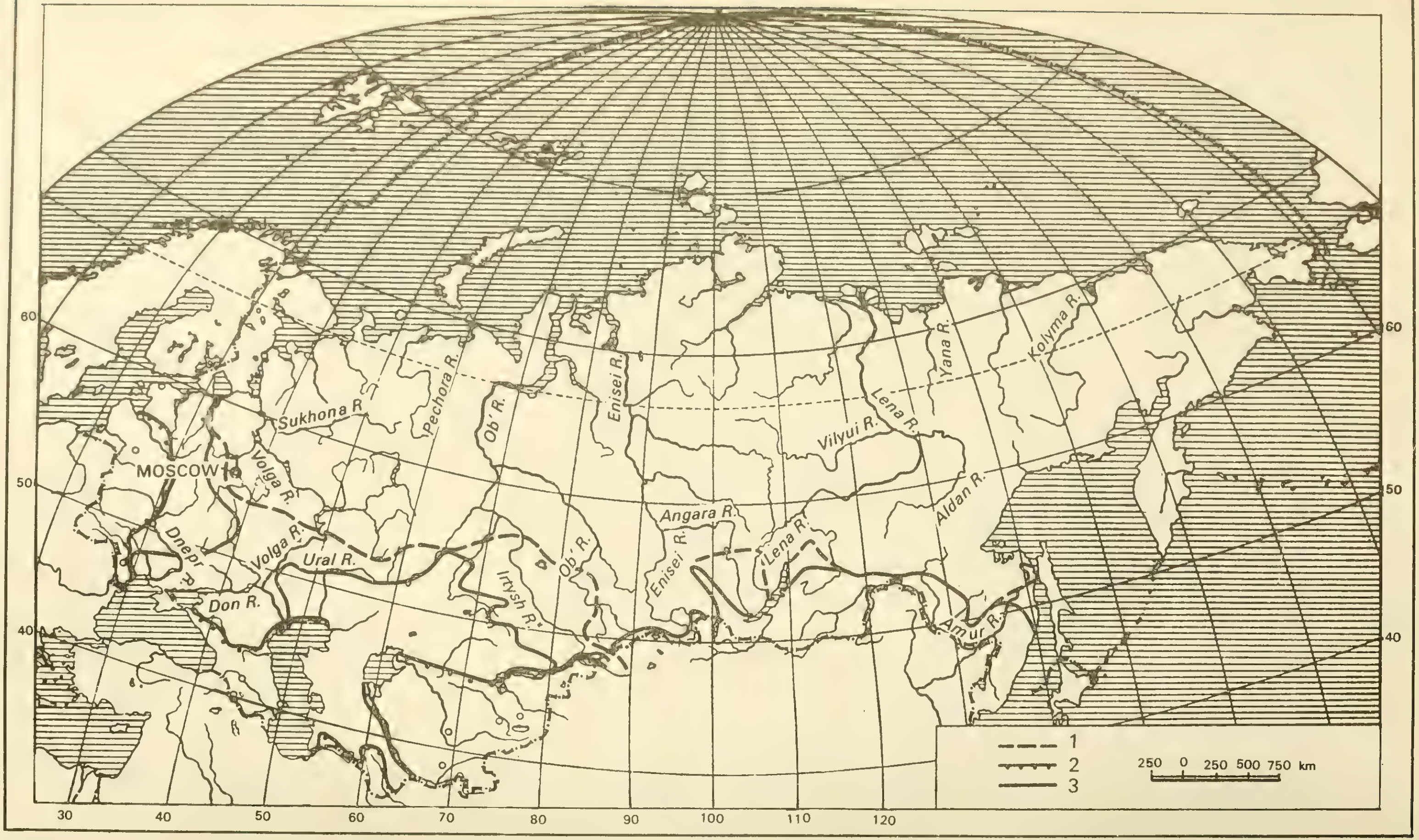
Reconstructed geographic range. The reconstructed northern boundary of the range of wild boar commences in the west at the eastern tip of the Gulf of Finland and southeast coast of Lake Ladoga (Mga region).[13] This is the northernmost point of habitation of wild boar in the USSR (60° N lat.). From there the boundary steeply turns south to Novgorod and farther into the region of Lake Peno and the town of Ostashkov to the environs of Kalinin. From there the boundary sharply descends south running through the western fringes of Moscow district or even Moscow (intrusions). Finally, the boundary proceeds toward Kaluga and turns to Tula, running later to the east, probably south of Ryazan'.

It is highly possible that wild boar occupied forest sections south of the Oka ("Trans-Oka Stockade"). From Ryazan' ("Ryazan' principality") the boundary of the range inexplicably turns east through Penza district ("Penza province," 18th century) and runs toward the Volga at Samarsk Luka or, probably, even more northward (wild boar is indicated in "Simbirsk province"). Wild boar reached its northern limit on the Volga probably by penetrating from the south, evidently along valleys of rivers like the Don and its tributaries (Khoper). At places far removed from the rivers the boundary could lie more to the south.

34 East of the Volga the northern boundary of the range of wild boar runs from Zhigula (or Ulyanov district) toward the Buzuluk River, southern Ural, Ik, and Sakmar, then to the upper reaches of

---

[13] The present discussion pertains to wanderers and not permanent habitation. The separation of the region of wanderers from that of regular habitation is very difficult. The references here pertain to peripheral points where the animal is found irrespective of the nature of its habitation unless specifically stated otherwise.



60
50
40
30
40
50
60
70
80
90
100
110
120
MOSCOW
Sukhona R.
Pechora R.
Ob' R.
Enisei R.
Lena R.
Vilyui R.
Yana R.
Kolyma R.
Aldan R.
Angara R.
Volga R.
Ural R.
Irtysh R.
Dnepr R.
Don R.
Amur R.
1
2
3
250 0 250 500 750 km

Fig. 7. Distribution of wild boar (*Sus scrofa* L.) in the Soviet Union (scale in km).

1—reconstructed northern boundary of geographic range where it does not coincide with boundaries established in mid-1950's; 2—boundary of range in 1930; 3—boundary of range in 1950's. V.G. Heptner.

the Beloe (Voznesensk Zavod—Irgizla; Kirikov, 1935). In the southern Urals wild boar reached in the north up to 52° or almost 53° N lat.[14] After crossing the southern extremity and foothills of the Urals, the boundary in Trans-Urals runs toward Bashkir preserve (west of Magnitogorsk) and Magnitogorsk and rises northeast toward 55° N lat. There wild boar has been recorded on the line between Miass (west of Chelyabinsk) and Kurtamysh (slightly south of Kurgan) at 55° N lat. or slightly more northward. More eastward the northern point of habitation of wild boar lies at Mangut railway station at 55°45′N lat., southeast of Ishim town and even slightly more north to the east to Ishim town (Lakes Ik and Kuban, a little north of 56° N lat.). Farther away, the boundary crosses the Irtysh and Ust'-Tara at 56°33′N lat. and runs between the Irtysh and Ob' (Barabin steppe) covering Lake Chany and probably its basin, i.e., along 55° N lat. or slightly more north almost along 56° N lat.

From the eastern part of Barabin steppe (Novosibirsk region) the boundary of the range turns sharply south into the region of the confluence of Biya and Katun, i.e., it almost approaches the Altai range. From there the boundary line encircles the Altai, turns south-east, passes into Zmeinogor region, and southward passes through the basin of the Tigerek River and, evidently, also Tigerek mountains or a part of them. Farther away, joining the Altai from the south, it proceeds southeast and east through the basins of the Shul'ba, Ul'ba, and Bukhtarma, and extends into China.[15]

Small sections of the southern Altai-Chuisk steppe (upper reaches of the Chuya with the center in Kosh-Agach) and the Kuraisk steppe (below, along Chuya in the region of 87°40′ to 88° E long.) and the upper reaches of Bashkaus (Chulyshman tributary) also fall in the range. Throughout this region wild boar was seen evidently only periodically as transgressions from Mongolia.[16] Farther away in the east the range covers all of Tannu-Ola up to its eastern extremity (Sangilen range) and the montane parts of Tuva in the upper parts of Little (Ka-Khem) and Great (Bii-Khem) Yenisei in the north up to the tributaries of the Great Yenisei, Azas, and Khamsara (the latter runs from the southern slopes of Udin range to the point of its confluence with Okin), adjoining Pri-Kosogol district of Mongolia. The Tuvin section of the habitat in the south as well as in the east is associated with the range of wild boar in Mongolia and evidently forms a common unit with it. Within the Soviet Union it is isolated by high mountains or only weakly linked with the section of the habitat of the animal more to the north.

---

[14] It is possible that the boundary beyond the Volga traverses somewhat even more northward than pointed out above but this is not supported by reliable data. Information about habitation up to Kama and Elabuga in Kama (Sludskii, 1956) is not sufficiently accurate and pertains to a long-past period (the ancient Anan'insk township). The line of reconstructed northern boundary of the range in the European part of the USSR differs greatly from that proposed recently (Sludskii, 1956) and ran very far north from Ladoga through Rybinsk reservoir, north of Kostroma, through middle Unzha, middle Vetluga, lower Vetluga, and Beloe estuary. The relative absence of wild boar at Vetluga even 1,000 to 2,000 years ago is a direct inference (Formozov, 1946).

[15] Wild boar were also encountered evidently along the mountain slopes surrounding the valley from the north (Muyuta River; Kolosov, 1939) but the assumption of their habitation on northern slopes of Katun range (Sludskii, 1956) can hardly be substantiated.

The habitat of wild boar on the northern slopes of the eastern Sayan and to the north of this commences in the west, in the basin of the upper reaches of the Kungus tributary of the Kan (about 95°40′ to 96° E long.). Its southern boundary runs along the northern foothills and the slopes of the above mountain system through the upper reaches of the Tagul and Biryusa, upper reaches of the system the Uda, Ii and Oka, Bol'shaya and Malaya Beloe, Kitoi and Irkut, encompassing the Tunkin range and passing along Irkut right up to Lake Baikal. This is indeed the southern boundary at present. No data are available about its former location but probably it differed little from that described above. There is very little information
35 about the northern boundary of the former habitat at Baikal. It may be assumed to have extended to the Angara around 57° N lat. (edge of Dolgii region) from a more western section than indicated, possibly through Taishet region. Turning from there toward Baikal the boundary evidently inclined considerably south but covered the upper reaches of the Lena in the north up to Ust'-Ilga and even Ust'-Kut (56°30′N lat.; transgressions). Farther away, the Baikal shore right up to its southwestern extremity formed the boundary.

In southern Baikal and beyond the boundary is now formed by the southern and eastern shores of the lake. From its northern extremity (probably from the upper reaches of Barguzin) the boundary proceeds north reaching Bodaybo region (northernmost point of the habitat in Siberia, around 57° to 57°30′N lat.). From there, the boundary inclines slightly south and proceeds east into the source of the Chara (57° N lat.). In the east it runs in the upper reaches of the Nyukzha River, a tributary of the Olekma, and proceeds along 54°45′N lat. to the Ol'doe (Amur tributary). From there the boundary descends somewhat south and encircles the Tukuringra range from the south, passing along its slopes and intersecting the left tributaries of the Urkan River, a tributary of the Zeya, at 54°20′, 54°30′, and 54° N lat., and leaving the Zeya slightly south of 54° N lat. Farther east the boundary descends even more southward, intersects the upper reaches of the Bureya, encompasses the lower and middle reaches of the Urma and Kur', and turning parallel to the course of the Amur runs to the Gorin River slightly south of Lake Evoron. Beyond the Gorin the range extends along the Amur up to 51°30′N lat. (up to the estuary of Khazelakh River), encompasses the region of the rivers Yai and Kod and Lake Kiza, and runs toward the Tatarskiy Strait at De-Kastri or slightly more south of it (Schrenk, 1859). It is possible that in the region south of the Gorin wild boar was an irregular visitor or an intruder.[17]

---

[16] As a rare exception wild boar might possibly occur even farther north, deep inside the Altai taiga, since the skull of a wild boar was found in Lake Telets (Kamgin Bay; Zalesskii, 1934).

At Sakhalin wild boar is absent and was probably never present even in the historic past. Fossil wild boar have reportedly been found there, however.

The natural range of wild boar in the Soviet Union is essentially a single continuous area, the gaps in the Altai-Sayan mountains being altogether insignificant; connecting points occur in the south in the immediate proximity of the present boundaries.[18]

South of the above northern boundary the range extends everywhere up to state boundaries and up to the coasts of the Azov and Black Seas and Crimea (in montane Crimea wild boar disappeared only in the middle of the nineteenth century) and even beyond them. The high montane areas of the Great Caucasus, Trans-Caucasus, Pamir, Pamir-Alai and Tien Shan, some mountains of Siberia, and

---

[17] According to other data for the middle of the last century (Maak, 1859), the range extended beyond the Gorin for an extremely short distance; the boundary on intersecting this river soon turned southeast and ran onto the right bank of the Amur slightly below the Gorin estuary. Running in the same direction, it extended toward Tatarskiy Strait south of Kiza.

[18] The boundary of the reconstructed range has been ascertained from Kalnin'sh, 1950; Ling, 1955; Nasimovich, 1955; Formozov, 1947; Satunin, 1895; Barabash-Nikiforov, 1956; Ptushenko, 1937; N.A. Severtsov, 1950; Kirikov, 1952 and 1955; Rychkov, 1762; Pallas, 1786; Eversmann, 1850; Gebler, 1837; Zalesskii, 1934; Makarov, 1949; Kolosov, 1938 and 1939; Yanushevich, 1952; Favorskii, 1936; Podarevskii, 1936; Kopylov, 1948 and 1950; V.N. Skalon, Shcherbakov, and Bazykin, 1941; V.N. Skalon, 1951; Maak, 1859; Rul'e, 1845; Middendorff, 1869; Radde, 1862; Gassovskii, 1927; Bannikov, 1954; Schrenk, 1859; Abramov, 1954; Serzhanin, 1955; and other sources; and according to material compiled by Nasimovich, 1955; Formozov, 1946; and Sludskii, 1956.

Sikhote-Alin form gaps in the range. The central and deep interior parts of the desert (Karakum, Kyzylkum, and others) do not fall within the range although in winter, when moisture is abundant, wild boar in some places colonize areas deep (up to 100 to 200 km) inside the desert (V.G. Heptner; Sludskii, 1956).

Wild boar belongs to the group of ecologically versatile species. As a common animal it is capable of withstanding very low temperatures and surviving in areas with mean January temperatures of up to 20 to 25°C and even 30°C [below zero].* At the same time, because of its short legs and consequently its ability to utilize only food lying on the ground (or in it), its distribution is associated with some definite conditions of snow cover; it cannot normally exist in areas with a very high snow cover.[19] A snow height of 30 to 40 cm and not more than 50 cm, appears to be the limit.

36 In the European part of the USSR the range boundary at some places coincides very precisely with the isoline of 50 cm snow depth. This line determines the boundary in the northwest between Ryazan' district and the Volga and from the Volga to southern Urals. The significant diversion of the range boundary south in the area between the Volga and Oka Rivers and its position south of the Oka are due to excessive snow in this region. In Siberia, due to the extreme severity of environmental conditions, such correlations are more complex and less distinct and the picture in some respects less clear than in European USSR. However, the distinct curvature in the boundary to the north in the Baikal and Trans-Baikal regions coincides with the poor snow in these regions, while the descent of the boundary to the south in the Amur and Ussuri regions, on the contrary, correlates with the occurrence of heavy snow and so on.

In addition to the association of wild boar with snow, the influence of other factors on the range is also significant (see the section "Biology"). In a geographic sense it is particularly significant that the animal succumbs to destruction by man most easily in regions with abundant snow and mostly in years of particularly heavy snowfall. All this occurs mainly in the northern, primarily in the borderline regions of the habitat of the animal, which in many cases could explain the boundary fluctuations of wild boar and its general recession.

Geographic range in 1930. The range described above, as pointed out, underwent intense shrinkage during the last century. The reason for this was destruction of the animal through thoughtless hunting. Natural causes, i.e., climatic fluctuations (considering the phenomenon as a whole), per se played a minor role or acted only as factors promoting destruction.

---

*Unspecified in Russian original—Sci. Ed.

[19] For information on the correlation of the range with snow see Middendorff, 1869; Podarevskii, 1936; Formozov, 1946; Abramov, 1954; Nasimovich, 1956; Sludskii, 1956; and others.

The recession of the northern boundary and the reduction of the range proceeded fairly rapidly, but became particularly intense from the middle of the last century. The process reached its culmination during the first one-third of this century. Boundary recession was least in the extreme northwest and Far East section of the range and comparatively insignificant in eastern Siberia. Recession was intense in western Siberia and Kazakhstan and significant changes occurred in European USSR (apart from the extreme western regions).

By the beginning of the 1930's, which could be considered the period of maximum reduction of the range, the area not only decreased notably, but that which was formerly a continuous zone disintegrated into a few individual discontinuous or even isolated portions. This is true of all European USSR and the Asiatic region in the east up to the Altai. Changes in the east were less significant or altogether absent.

The former zone of habitation of wild boar, as seen in 1930, covered far western parts of European USSR. Its northeastern boundary commenced roughly at Riga, turned toward Velikie Luki, and shortly before entering them turned south into Vitebsk or bypassed it from the west. Later, it ran east of Mogilev through Gomel' or somewhere between Gomel' and Bryansk (close to the former) and after covering the Chernigov region turned west, bypassing Kiev from the north. In a manner not precisely known it later turned southwest toward the upper Dnestr roughly at Mogilev-Podol. On its way to the Dnestr the boundary ran along the Black Sea and crossed westward along the USSR border into the estuary of the river along the sea coast (Bobrinskii, 1944; Formozov, 1946; Sludskii, 1956).

East of the above line demarcating the region, which represents a fairly permanent habitat of the animal, some rare encounters, sometimes at quite distant places, have been recorded. Thus wild boar have been sighted in Ostashkov region, Lake Peno, Smolensk, Bryansk, and even Moscow district.

The second habitat of wild boar covered the Caucasus and northwestern and northern banks (partly) of the Caspian Sea. The northern boundary of this part of the range ran from the Sea of Azov along Lake Kubana to Krasnodar, from there to Armavir, turning

around Mineral'nye Vody from the south, toward Prokhladnyi
38 (slightly northeast of Nal'chik). From there, along the Terek, the boundary ran right up to the sea. From the Terek estuary, in a strip along the sea coast, the range extended north into the Volga delta and farther east up to the Ural estuary. This zone was very narrow and bounded nearly exclusively by a zone of Caspian reeds. Only at some places, for example, in the lower reaches of the Kuma, did it enlarge giving rise to small pockets away from the sea. Moreover, this band of the range was interrupted at some places as, for example, in the stretch between the estuaries of the Kuma and Volga.

Beyond the Caspian Sea the range covered the Kopet-Dag, Great Balkhan, and the course of the Atrek except for its lower dried up part (roughly up to Lake Delili), the basins of Tedzhen and Murgab, and the extreme south of the interfluve of these rivers. Farther away the boundary covered the Amu-Darya from the state boundary to its left bank up to the Aral Sea and ran along the southeastern and eastern coasts of the Aral Sea up to the estuary of the Syr-Darya. From this river the boundary ran into the lower reaches of Lakes Sarys and Telekol'sk, encompassed the Chuya, ran along [Lake] Balkhash, and covering the Alakol', Tarbagatai, and the Zaisan depression, continued toward China.

Small isolated sections of fairly permanent habitations of wild boar have been preserved north of the above line in Kazakhstan. These sections were isolated from the main range and comprise the area of Lake Chelkar-Tengiz and the lower reaches of the Turgai and Irgiz, Lake Kurgal'dzhin and Tengiz southwest of Akmolin, and perhaps, Kamysh-Samarsk lakes and the lower reaches of the Uzenei[20] (Bobrinskii, 1944; Sludskii, 1956; V.G. Heptner).

Wild boar occurred in the southern Altai in the period under discussion only as an intruder in some of the areas mentioned above adjoining Mongolia.

In the Sayan, west of Baikal, at the commencement of the 1930's the northern boundary ran much southward than it does now, and the range in general represented a fairly narrow strip along the Sayan foothills. Thus in the region of Biryusa it fell far short of reaching Taishet and the Uda basin to the north and did not cross 54°33′ N lat. From the Ii, in the basin of which wild boar proceeded north roughly up to 54°10′ to 54°20′ N lat., the northern boundary turned southeast toward Baikal exiting on its southwestern extremity or slightly closer to the Angara estuary. However, swine intrusions have been reported at Angara (Kureika River, 54°45′ N lat.) and even at the sources of the Lena.

---

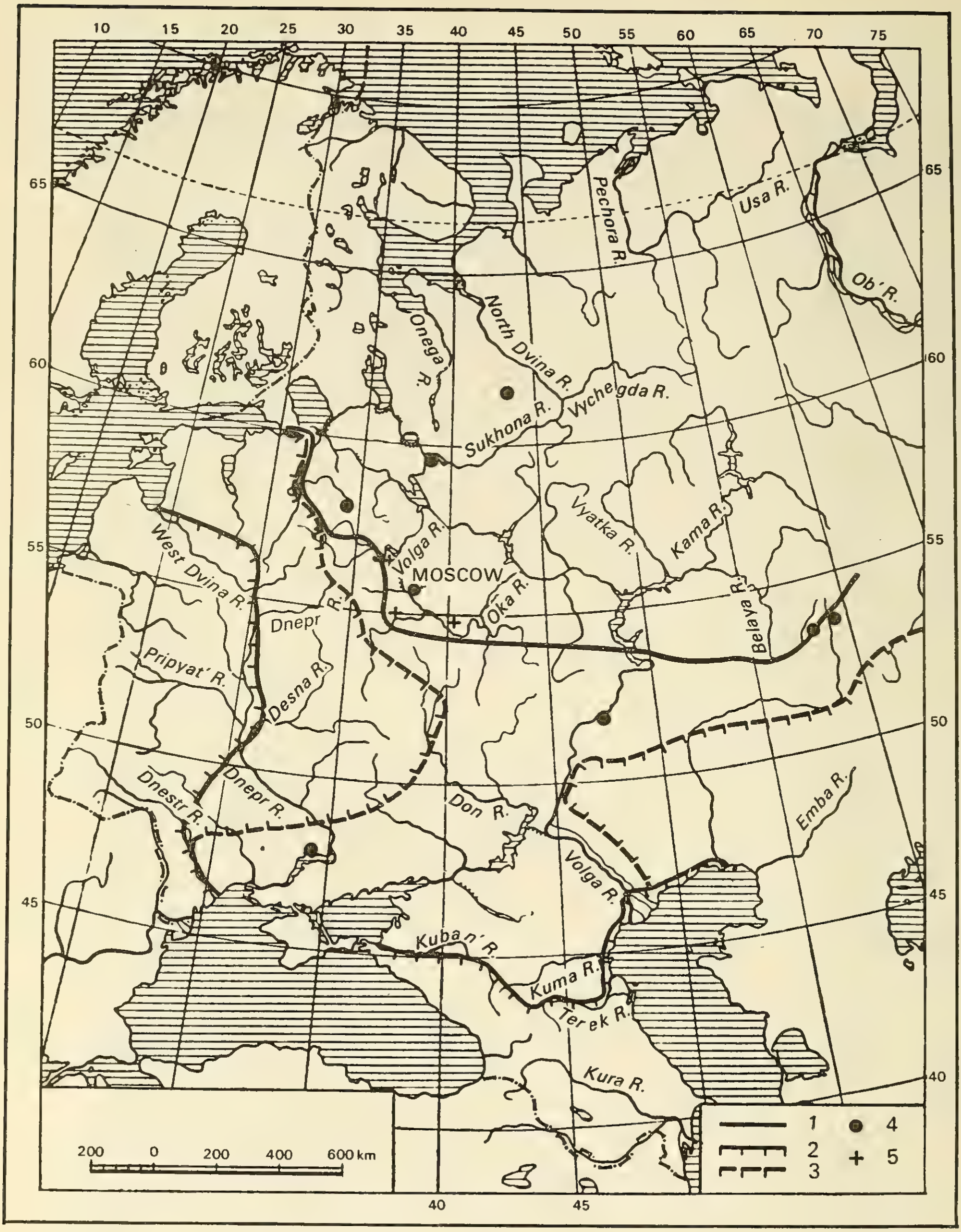
[20] In the region of the Ermentau highland wild boar was seen in the period under description only as an intruder from Kurgal'dzhin (Sludskii, 1956; map; pp. 168 and 185). Pockets of habitation there (ibid., map; p. 147) were evidently absent.

In trans-Baikal at this time the range boundary receded southward and did not extend north of Kalar 56° N lat.) where the animal was extremely rare. Also, it did not cover the upper Angara (Podarevskii, 1936; Kopylov, 1950; Troitskii, 1930; Skalon, Shcherbakov, and Bazykin, 1941; Skalon, 1951; Sludskii, 1956).

In the Far East changes in the geographic range in the 1930's were evidently relatively insignificant. Along the Amur the range did not extend up to Gorin estuary and the lower reaches of the river. It encompassed only its upper reaches without reaching Lake Evoron and the boundary crossed the Amur roughly around Komsomol. From there it turned southeast in a not-too-straight line and ran toward the Tatarskiy Strait at Botcha Creek and Koppa (around 48° N; Abramov, 1954).

Geographic range in mid-1950's. Following the extreme shrinkage of the boundary described above by 1930, significant increases in wild boar populations occurred in the 1940's and 1950's and its range expanded considerably. Wild boar once again began to occupy territory they had inhabited in the past. Part of this process commenced even in the 1930's. The main reason was curtailed persecution of the animal and in some places its protection and regulation of hunting. The least positive changes in the range occurred in Siberia east of the Altai and in the Far East. Here the present-day range (mid-1950's) generally corresponds to that shown above for the period around 1930.

39 Particularly significant changes in the range in the positive sense occurred between the 1930's and 1950's in European USSR, Kazakhstan, and parts of southwestern Siberia. Artificial shrinkage of the range was very intense and, obviously, the possibilities of its restoration limitless. Restoration is occurring right before our eyes as a matter of fact, with different stages observable in different places. In some sections of the range wild boar are already well restored and the animals present in significant numbers. Other sections are in the process of being inhabited but as yet do not contain a large number of animals. In still other sections animals are found infrequently, in other sections rarely, and so on. Intrusions which for relatively stable boundaries are not significant in understanding range dynamics, are of great importance in the present case as an index of the tendency toward expansion and restoration of the range, and the routes and directions of its future limits. From this viewpoint the present range map of wild boar is of general interest. The boundaries given


10
15
20
25
30
35
40
45
50
55
60
65
70
75
65
60
55
50
45
40
Pechora R.
Usa R.
Ob' R.
North Dvina R.
Onega R.
Vychegda R.
Sukhona R.
Vyatka R.
Kama R.
Volga R.
MOSCOW
Oka R.
West Dvina R.
Dnepr R.
Pripyat' R.
Desna R.
Belaya R.
Dnestr R.
Dnepr R.
Don R.
Emba R.
Volga R.
Kuban' R.
Kuma R.
Terek R.
Kura R.
200
0
200
400
600 km
1
2
3
4
5

37 Fig. 8. Boundaries of distribution, places of transgression, and places of acclimatization of wild boar (*Sus scrofa* L.) in European USSR (scale in km).

1—reconstructed northern boundary of range; 2—boundary of range in 1930; 3—boundary of range in mid-1950's; 4—distant transgressions of wild boar after 1930—in the west, reckoning from the north; Rovdin region (dubious), Ulom River, Vyshnii Volochek, and Kamensk-Dneprov; in the east: Bashkir preserve, Agapovo at Magnitogor, and Vol'sk on Volga; 5—some places of acclimatization of wild boar between 1950 and 1960 (Zavidovo, Serpukhov, Solotcha, and Vyksa). V.G. Heptner.

below also take into consideration the limits of intrusions (apart from some particularly distant ones which are specified) and provide an idea of the status in the mid-1950's.

The boundary of the western habitat of wild boar in European USSR in the northwest proceeds initially along the reconstructed boundary described above, commencing at the southwestern bank of Lake Ladoga up to Ostashkov region and Lake Peno. From there it turns south toward the Nelidov region and, inexplicably, probably east toward the boundaries of Moscow district,[21] i.e., encompassing the greater part of Smolensk district, probably including Vyazma, and proceeds into Sukhinichei region (southwest of Kaluga). From there, turning southeast, it proceeds towards the Lipets region, about 40 km south of Lipets, Voronezh (Voronezh preserve), and the Voronezh estuary into the Don. It then proceeds about 80 km west of Liski (Ukolov region) and, turning slightly southwest, to Valuek (Nikitov region, directly northeast of Valuek) (Melander, 1939; Barabash-Nikiforov, 1956; Sludskii, 1956).[22] Thus, the boundary encompasses from the east almost all of Smolensk district, a significant part of Kaluzh, possibly south of Tul'sk, the entire Orlov region, and western part of Lipets, Voronezh, and Kur' districts.

The range boundary of wild boar in the Ukraine can only be generalized. It covers the eastern part of Kharkov district (Sludskii, 1956) and in the south Poltava, Kiev, Kirovograd, and Vinnits districts (Korneev, 1952). Evidently the boundary from Valuek region runs southwest and encompasses the northwestern half of Kharkov district and later turns steeply west-southwest, intersecting the Dnieper somewhere above Dnepropetrov and running toward the Dnestr evidently in Soroka district. From there, it descends along the river to the sea and runs along the coast into the estuary of the Danube River.[23]

---

[21] Sightings in Moscow district reported recently are not taken into consideration here since they are associated with migrations of animals released there for acclimatization in Zavidovo (see below). In any case, even if there are some transgressions from the west, it is difficult to distinguish them.

Recently, some deep intrusions of wild boar are known in the more northern part of the range, i.e., in the region of Vyshnoi Volochek and in the region between Lake Beloe and Kuban and Rybinsk reservoirs (Ulom region of Vologod district; Nasimovich, 1955). The latter falls roughly 400 km of the nearest segment of the recent eastern boundary. It has been suggested that these represent deep intrusions of animals acclimatized in the southern part of Kalinin district. Also, there are cases (Kholostov, 1956) of catches of wild boar (January, 1953) even farther away in the northeast in Rovdin region, Arkhangel'sk district (in Vage above Shenkur, V.G.), roughly 650 to 700 km away from nearest boundary. Evidently the reference here is to a solitary animal. The age of the animal, about 2.5 years, also supports this view. (V.H.)

[22] The assumption is unfounded that wild boar in Podon'e could have appeared not only from the west but also due to dispersal of animals released for acclimatization in Ryazan' district (see below) (Barabash-Nikiforov, 1956; Sludskii, 1956). The animals, firstly, were settled far in the north and, secondly, all of them perished. There is no doubt that the range expansion in Don basin is the result of animals spreading from western districts.

40 It can be seen from the above review that over the past 20 to 25 years the boundary moved eastward a distance of up to 250 or even 600 km. In the northern section it has already regained its natural range (coinciding with the "reconstructed boundary") over a significant area (north of Ostashkov). This is not so for much of the range. The western section within the USSR continues to remain isolated from the rest, primarily from the Caucasian sector.

The Caucasian part of the range from 1930 onwards did not expand perceptibly north, the boundary from the Azov coast to the Volga remaining essentially stationary.

An extremely intense and rapid expansion of the range and a northward shift of the boundary occurred in the area from the Volga to the Altai. In the area between the Volga and Ural wild boar, evidently from the Caspian reeds, colonized the region of Kamysh-Samarsk lakes and the lower reaches of Uzen' and from there have spread even farther. The points at which the animals penetrated this region are the Bykov farmstead on the Volga (Bykov, south of Kamyshin), the region of Pallasovka (east of Kamyshin), the lower reaches of Eruslan (Valuek region), the region between the Volga and the southern tributary of Eruslan-Torgun (i.e., area east of Kamyshin), and even Vol'sk. Somewhat more to the east wild boar have been sighted along the Chizhin flood zones (between Bolshoi Uzen' and Ural'sk) and at the Ural (Stroganov, 1954; Zaletaev, 1952; Sludskii, 1956). The encounter at Vol'sk is an intrusion quite isolated from the remaining ones. It is significant that wild boar do not breed along Volga and the intrusion at Bykov farmstead occurred from the east, from the steppes, and not along the river valley from the south. Along Ural River the animals spread from the sea to Ural'sk.

From the Ural the boundary turned into the lower reaches of the Ilek into Burannyi region and turning round the Ural and its bend from the south, ran into Adamovka region (Adamovka, northeast of Orsk). A particularly distant transgression was noticed at a place slightly south of Magnitogorsk (Agapovka). From Adamovka, the boundary ran northeast, crossed the Tobol, and running along the lakes lying along its right bank, somewhat east of Kustanay, turned to the north reaching Kosulin region (southwest of Kurgan at 64° E long. and roughly 55° N lat.—V.H.). This was the northernmost residence of wild boar in this part of the country. The natural range here had almost been restored or the animal came very close to the former northern boundary.

---

[23] In the Dnieper basin bodies have been sighted in river floods at Kamensk-Dneprov Kamensk (Sludskii, 1956).

From Kurgan the boundary turned east-southeast toward Petropavlov. From there the boundary line becomes extremely complex and less well defined. From Petropavlov the boundary proceeded directly to the south, and, having reached roughly 52°N lat., turned sharply east and exited at Ermentau highland (Ermentau; at 52° N lat. or slightly more north, directly north of Akmolinsk; see footnote on p. 34). From there, going round Akmolinsk in the form of an arc from the west, the boundary line passed through the upper reaches of the Nura and slightly northeast of Karaganda, encompassed Karkaralin and Chingiztau mountains, and ran to the eastern tip of [Lake] Balkhash. From there it turned northeast, covering the Tarbagatai, the Zaisan district, and the southern slopes of Kurchum range, and ran into China.

Sometimes wild boar extended far beyond the limits of the above region into Bayan-Aul region, Maisk (at Irtysh below Semipalatin), into the environs of Semipalatinsk, Krasnyy Kut, at the point of intersection of the Irtysh and 76° E long. and even the Irtysh below Krasnyy Kut. Intrusions were known in Bukhtarma valley, Srosten pine forest in the Altai steppes (northeast of Rubtsov), toward the confluence of Biya and Katun, and in other places of pre-Altai steppes.

As can be seen from the data presented thus far, in the past 20 to 25 years (commencing from 1930) the habitat of wild boar between the Volga and Altai has expanded sharply. In Kazakhstan expansion was particularly intense from 1941. From the beginning of the war a sharp reduction in hunting of wild boar took place, and a humid period set in again so that all the reservoirs which had dried up
41 became favorable habitats once more for animal life; they filled with water and various types of reeds and cattails grew on the shores. These factors and subsequent regulation of hunting led to an expansion of the range of wild boar.

Over the last 20 years the habitat of wild boar has tripled in Kazakhstan, covering territory where it was absent 100 to 150 years ago. It has colonized once again not only the steppe but the forest-steppe zone. In the western and central part of the area under description the present-day northern boundary of the range has already come close to the former natural ("reconstructed") boundary and at one place even reached it. In the east, as shown by intrusions (see

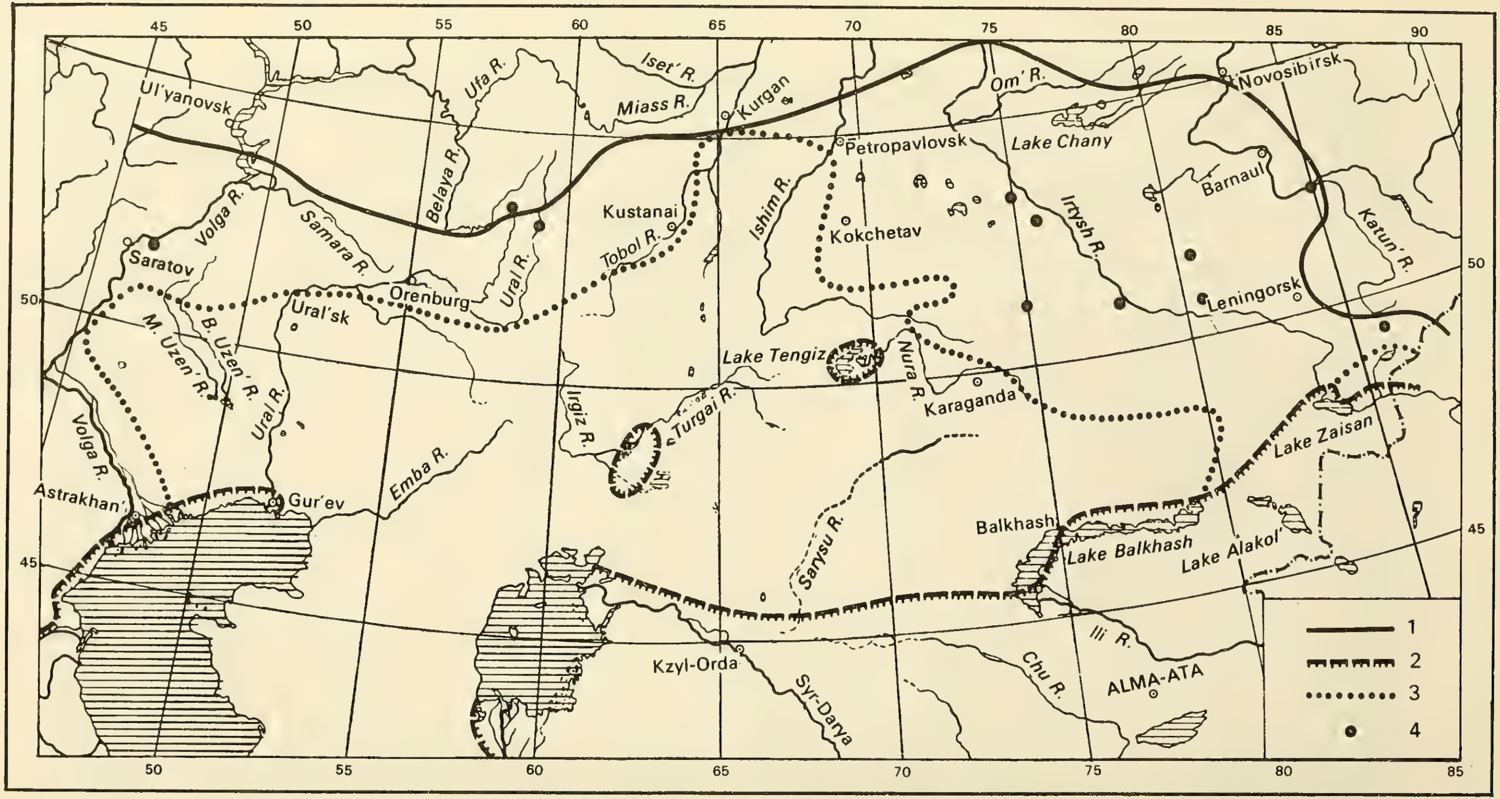

45
50
55
60
65
70
75
80
85
90
Ul'yanovsk
Ufa R.
Iset' R.
Miass R.
Kurgan
Om' R.
Novosibirsk
Lake Chany
Petropavlovsk
Barnaul
Belaya R.
Kustanai
Ishim R.
Kokchetav
Irtysh R.
Katun' R.
Saratov
Volga R.
Samara R.
Ural R.
Tobol R.
Orenburg
Ural'sk
Leningorsk
M. Uzen' R.
B. Uzen' R.
Lake Tengiz
Nura R.
Karaganda
Turgai R.
Irgiz R.
Lake Zaisan
Emba R.
Gur'ev
Astrakhan'
Sarysu R.
Balkhash
Lake Balkhash
Lake Alakol'
Ili R.
Kzyl-Orda
Syr-Darya
Chu R.
ALMA-ATA
1
2
3
4

Fig. 9. Geographic range of wild boar (*Sus scrofa* L.) in Trans-Volga, Kazakhstan, and western Siberia.

1—reconstructed northern boundary of range; 2—northern boundary of distribution in 1930; 3—northern boundary in mid-1950's; 4—deep transgressions of wild boar after 1930 (Vol'sk; Bashkir preserve; Agapova near Magnitogorsk; Bayan Aul, Irtysh, Krasnyy Kut, and Maisk regions; Semipalatinsk town near Irtysh; Bukhtarma; confluence of Bia and Katun Rivers; and Srosten pine forest at Rubtsov). V.G. Heptner.

map), the very same process has occurred, although it has not attained the same intensity.[24]

The rate of colonization of wild boar, especially in the 1940's, was extremely high at some places. Over a period of two to five years in some parts of Kazakhstan wild boar have spread 300 to 500 km (in a straight line), moving roughly at an average of 100 km each year. Colonization has proceeded mainly along river valleys and lake systems.[25]

On the whole the expansion and reconstruction of the range of wild boar in the area under description was more significant than in the west. This is simply explained by the low population density in Kazakhstan and adjoining places.[26]

The expansion of this part of the range led to its merger in the Soviet Union with the Caucasian sector. However, the separation of eastern and western parts of the range is still total and very distinct. There is no possibility, at least not in the near future, of the two ranges merging, but the eventuality cannot be totally ruled out. A tendency to merge from both sides is discernible.

As for the areas of distribution of wild boar in southern Altai (only stray occurrences), in Tuva, the Sayans and farther east, apparently no tendency for expansion and restoration of the range has been detected in the last decade.

For purposes of acclimatization wild boar were released for hunting in the last decade in Serpukhov and Zavidov near Volzh reservoir northwest of Klin (Kalininsk district), Solotcha region on the left bank of the Oka slightly north of Ryazan' (Ryazan' district), and in Vyksa region on the right bank of the Oka slightly south of Murom (Arzamas district). Zavidov wild boar survived until 1955 and settled to some extent especially in Klin region of Moscow district. It is possible that it was from here that stray intrusions were reported in Vyahnei Volochek and Ulom region. Solotchin wild boar, left to their fate in a highly snowy district (Zavidov boars survived), died out completely by 1950's.[27]

---

[24] It is premature to assume that wild boar in Kazakhstan has "completely" regained its former geographic range (Sludskii, 1956).

[25] Propagation of wild boar between the Volga and Altai cited from data of Sludskii (1956).

[26] As a result of cultivation of virgin land the situation may undergo intense and rapid changes.

[27] The suggestion that animals from here were seen in the upper reaches of the Don (Sludskii, 1956) has no basis (see above).

Vyksa wild boars were still surviving in the early 1950's but evidently are condemned to die.

Geographic Range outside the Soviet Union

The extensive range outside the Soviet Union has been shown in Fig. 4. In Africa it includes Rio de Oro (Spanish Sahara), Morocco, Algeria, and probably Tunisia (at present, however, wild boar are absent there), Egypt (disappeared around 1900), and Sudan (Kordofan and Sennar). In Europe the range covers all western Europe including the British Isles (extinct), Corsica, Sardinia, and Sicily. In the north the range is bounded by the Baltic Sea but also covers the southern part of the Scandinavian Peninsula (extinct). The Asian range of wild boar includes Asia Minor, Syrian zone of United Arab
43 Republic and Palestine, Iran, Afghanistan, India, Baluchistan, Kashmir, Nepal, Ceylon, Burma, Indochina, Malacca, Andaman and Nicobar Islands, Sumatra and adjacent tiny islets, Java and the entire chain of Sunda islets in the east including Flores, Sumba, Banks, Sumbawa, Timor, and Rota. Farther away the range covers Aru and Kai, New Guinea, Louisiade, Solomon Islands, Bismarck Islands, Admiralty Archipelago, and some islands on the western part of New Guinea—Yapen, Misol, Barenta, and others, including Vaigeo and Seram Islands. In the north the range covers Hainan, Taiwan, and all the islands of Japan, including Hokkaido and Ryukyu.

On the mainland the range covers northeastern, eastern, and southeastern China far south. In the west, in this part of China, the range covers Szechwan, Shensi, and Kansu almost up to Kukunor. In Mongolia wild boar occur in Hentei roughly up to 47° N lat. to the south, Sayan and Altai region, Khangay in the south roughly up to 46° N lat., and the Mongolian Altai to the south up to 44° N lat. In northwest China the range includes the Tien Shan system, Tarim and Yarkand basins, and extends toward the mountain system of Dzhungaria district. In Inner Mongolia, in the desert region of northwestern China and Tibet, wild boar are absent and were never present. Wild boar are already extinct in several places apart from those indicated above.

Wild boar are either acclimatized for hunting or have become feral (Chinese domestic swine) in some places in the United States (Tennessee, North Carolina, Georgia, Texas, California, New Hampshire) and in several places in Central America. They have similarly acclimatized at two places in Argentina and settled there rather rapidly. (V.H.)

Geographic Variation

The geographic variation of the species in the area under discussion is very high and 26 to 28 forms are recognized.

The number of varieties is extremely large, exceeding 50. The actual number of subspecies, however, is undoubtedly less than 26 to 28, since a large number of descriptions are unsatisfactory and the intraspecific variation of the species has never been revised.

In the Soviet Union there are five subspecies which differ slightly in some details of craniology, mean body and skull size, and dominant color type.[28]

1. **Central European wild boar** (*S. s. scrofa* Linn., 1758) (syn. *falzfeini*).

Size, medium. Maximum skull length 370 to 410 mm. Color dark and fur rusty-brown. Lacrimal long and relatively narrow. Third upper molar relatively long; talon well developed and partly forms third transverse row of tuberosity.

Found in west European USSR. Outside the USSR found in central and western Europe. Relationship with other subspecies in the context of its range and some other characteristics not clear.

2. **Rumanian wild boar** (*S. s. attila* Thos., 1912).

Size, large. Maximum skull length 410 to 470 mm. Color dark but lighter than that of preceding form. Lacrimal long. Third upper molar same as in preceding form.

Found in the Caucasus, Trans-Caucasus, and along northern Caspian coast. In some respects wild boar of the Ukraine and eastern part of Belorussia and probably of southwest Turkmenia also belong to this form. Outside the USSR, apart from Rumania, also evidently found in Hungary, the Balkans, Asia Minor, and northern Iran. Relationship to *S. s. lybicus* Gray, described from southwest Asia Minor, also not clear.

3. **Middle Asian wild boar** (*S. s. nigripes* Blanf., 1875).

Size, generally quite large but range of variation quite high. 44 Color light, lighter than rest of subspecies, and stands out in contrast to black color of legs. Fur lighter than in western forms. Lacrimal shorter than that of preceding forms, and facial portions of skull somewhat shortened. Third upper molar as in European forms but sometimes simpler.

---

[28] According to Adlerberg (1930) and Fetisov (1956), with modifications.

Found in Middle Asia and Kazakhstan. Outside the USSR found in eastern Tien Shan, western Mongolia, Kashgar, and possibly Afghanistan and southern Iran.

4. **Trans-Baikal wild boar** (*S. s. sibiricus* Staffe, 1922) (syn. *raddeanus*).

Smallest of wild boar forms. Maximum skull length of male 370 to 400 mm. Color dark brown, almost black. From posterior edge of mouth, along cheek to pinna, gray or grayish-whitish patch up to 24 cm in length occurs. Skull shortened and high; lacrimal almost squarish. Third upper molar short and relatively broad; talon poorly developed and simpler than in European forms.

Found in Baikal and Trans-Baikal. Outside the USSR found in northern and northeastern Mongolia. Relationship of this form to the form *canescens* Heude, described from near Peking, is not clear; Manchurian wild boar are not related to this form.

5. **Ussuri wild boar** (*S. s. ussuricus* Heude, 1888) (syn. *continentalis, gigas*).

Largest of USSR swine and of species as a whole. Maximum length of male skull 490 to 510 mm. Color variable but mainly dark; new coat dark brown or almost black. From corner of mouth to ear distinct white band present (G.F. Bromlei). Lacrimal somewhat shortened but longer than in Trans-Baikal form. Third upper molar broad.

Found in Ussuri basin and Amur in the west to Great Khingan. Evidently this form inhabits northeastern China and the forms described here, *songaricus* Heude (Sungari valley) and *mandchuricus* Heude (Mukden), must also be placed as its synonyms.

The number of wild boar forms described from parts of the range falling outside the USSR is very large, more than 20. This number is made up of not only the subspecies, which are geographically and morphologically close to the group *scrofa,* but also those which were formerly placed among other species but are now merged with the species *S. scrofa* (see above). With such an interpretation of the species, the morphological range of its geographic variability is considerable. Along with the giant forms of Europe, Amur region, and Manchuria, in the far south and especially in the island region of the extreme southeastern part of the range, there also exist small, often extremely small, forms. The extreme form is represented by Papuan swine which are no larger than a young pig.

Not all the forms have been described with adequate supporting information and there is no doubt that their actual number is fewer than currently asserted. Some forms of the island region of southeast

Asia evidently represent domestic swine turned wild, which were imported by islanders at various times from different islands.

At present the following subspecies of *S. scrofa* (Haltenorth and Trenze, 1956) are commonly recognized in Europe (in addition to forms *scrofa, attila,* and *falz-feini*—see above): *S. s. meridionalis* Fors.-Major, 1882 (Sardinia), *S. s. castillanus* Thos., 1912 (Iberian Peninsula), *S. s. reiseri* Bolkay, 1925 (Yugoslavia), and *S. s. majori* de-Beaux and Festa, 1927 (Italy); in Africa: *S. s. barbarus* Scl., 1860 (northwest Africa, Rio de Oro, Egyptian region of United Arab Republic and Kordofan); in Asia (in addition to *attila, ussuricus, sibiricus,* and *nigripes*—see above): *S. s. libycus* Gray, 1868 (southern Turkey and Palestine), *S. s. cristatus* Wagn., 1839 (India, Indochina, Burma, and Ceylon), *S. s. vittatus* Müll. and Schleg., 1842 (Sumatra, Java, Bali, Lombok, Sumba, Banka, and Sumbawa), *S. s. floresianus* Jent., 1915 (Flores), *S. s. timorensis* Müll. and Schleg., 1845 (Timor), *S. s. nicobaricus* Mill., 1902 (Nicobar Island), *S. s. andamanensis* Blyth., 1858 (Andaman Islands), *S. s. chirodontus* Heude, 1888 (southern China and Hainan), *S. s. taivanus* Swinhoe, 1868 (Taiwan), *S. s. riukianus* Kuroda, 1924 (southern islands of 45 Ryukyu archipelago), *S. s. leucomystax* Temm., 1842 (Japan), *S. s. koreanus* Heude, 1897 (Korean peninsula), *S. s. moupinensis* M.-E., 1871 (from Szechwan through Central China to Jehol), and *S. s. papuensis* Less, and Gerot, 1826 (extreme southeastern part of the range apart from the islands indicated above, with the center in New Guinea). (V.H.)

Biology

Population. The wild boar population has undergone sharp changes in different years. Fluctuations are determined in each individual district by litter size, migrations, mortality in severe winters, occurrence of infectious diseases, and intensity of hunting. In just a year or two a population can drop over a considerable area by 10%, doubling or trebling in the very next year (even without migrants).

Precise data on wild population and density in the USSR are few. The total number of animals in the Soviet Union is evidently a few hundred thousand. In Belovezh Forest in the 1890's and early twentieth century the population density ranged from 4.4 to 30.8, an average of 13.3 per 1,000 hectares (Kartsev, 1903); in the 1940's and 1950's it fluctuated between 4 and 19 (average 9.9) (Lebedeva, 1956). In the Astrakhan' preserve at the end of the 1930's the population density rose to 27 per 1,000 hectares (Lavrovskii, 1955), in the Caucasian preserve averaged 4 to 8 (Donaurov and Teplov, 1938), and in

Fig. 10. Broad-leaved forest, typical habitat of wild boar in Belovezh Forest. Photograph by A.G. Bannikov.

Bryansk district forests 0.5 to 4.2 (Fedosov and Nikitin, 1951). In years of abundant pine nut yield in Khentei (Mongolia), and evidently also in the Far East, population density rose to 30 to 40 per 1,000 hectares. In Kazakhstan and Central Asia along the banks of large lakes and rivers densities of up to 50 to 60 per 1,000 hectares are known in favorable years.[29]

46 As a result of sporadic migrations, for example, during forest fires or heavy snows, temporary concentrations of animals up to 200 to 300 per 1,000 hectares form in reed thickets along the banks of lakes over a few hundred hectares.

Throughout the eighteenth and the first half of the nineteenth century a reduction in population and range of wild boar took place. Population growth was recorded from the second half of the nineteenth century in Baltic region (Ling, 1955) and from the 1930's everywhere else (with the exception of some regions of the Caucasus, Trans-Carpathia, and Siberia). Restoration of the range occurred simultaneously (see above). Maximum population of wild boar was observed in the 1950's in the Volga delta, Syr-Darya and Chuya valleys, lower reaches of the Ili River, along the banks of Lake Zaisan, and in western Tien Shan mountains (Sludskii, 1956). In the Far East it was high along midreaches of Khor and Anyuya Rivers, along the Shukhi-Pokta range, along the northern spurs of the Little Khingan, on Iman and Bikin Rivers, and at the sources of the Bidzhan River (Abramov, 1954).

---

[29] In Germany at the end of the last century the population density of wild boar was 1.7 per 1,000 hectares; between 1936 and 1939 it rose to 5.2 when the total population was 66,000 (Oloff, 1951).

Before the commencement of the nineteenth century many wild boar lived in downstream valleys and reed thickets of steppe rivers (Dnestr, Dnieper, Don, and Danube). In the deltas of the Kuban, Volga, lower reaches of Kuma, Terek, and Kur' Rivers and along the coasts of the Caspian Sea wild boar are numerous even today.

Habitat. The diversity of diet of wild boar determines its extreme eurytopic character. It inhabits zones from boreal taigas to deserts. In mountains it may be found in all zones up to and including the alpine. In the Carpathians wild boar occur up to 1,900 m, in the Caucasus up to 2,600 m, and in the mountains of Central Asia and Kazakhstan up to 3,600 to 4,000 m. The importance of a given location for the species is determined by the abundance of food, its accessibility, and the protective conditions offered. With changes in seasonal and annual abundance of food sources, the importance of a place also changes. Nevertheless, some major locales are usually occupied by wild boar for most of the year, since they ensure food and offer hideouts to the animal. Other places are important only temporarily and still other areas always of secondary importance, being visited only periodically and by a small number of animals. In Europe deciduous and mixed forests currently serve as the main habitats of wild boar. Forests in which most of the trees are oak or beech and which enclose marshy sections and meadows serve as optimum habitats. Sites used periodically include meadows and cultivated lands. Thus in Belovezh Forest, in woods and in open sites 85.1% and 14.9% respectively of wild boar were counted over a period of four years. The main habitats in the region are represented by well-developed, broad-leaved, mixed forests and marshy mixed
47 forests. Periodically, in spring and autumn, meadows and farms are also used. Coniferous forests and undergrowths are of secondary importance (Lebedeva, 1956). Pure oak groves and beech forests acquire importance as habitats of wild boar only in those years when these species bear fruit.

In the montane regions of the Caucasus and Trans-Caucasus belts of beech and oak and other fruit-bearing forests are of primary importance for wild boar, which are found in them year-round (Din-

46 Fig. 11. Marshy forest, a favorite habitat of wild boar in Belovezh Grove. Photograph by A.G. Bannikov.

nik, 1910; Loginov, 1936; Donaurov and Teplov, 1938; Nasimovich, 1939; Markov, 1932, 1933, and 1934). In these forests, 37 to 62% of all the wild boar counted were found in the Caucasian preserve. Coniferous forests (8 to 55%) and subalpine zones (2 to 28%) play a secondary role, where wild boar usually live from July to September. The alpine zone is used by wild boar only occasionally during the five summer months and the occurrence rate is low (Donaurov and Teplov, 1938).

In the mountains of Middle Asia and Kazakhstan wild boar colonize all vertical zones. The main habitats are the lower parts of fir and deciduous forest belts. The latter acquire particularly great importance in the period of ripening of fruits and nuts. Tugais [vegetation-covered bottomlands] along mountain rivers and juniper forests

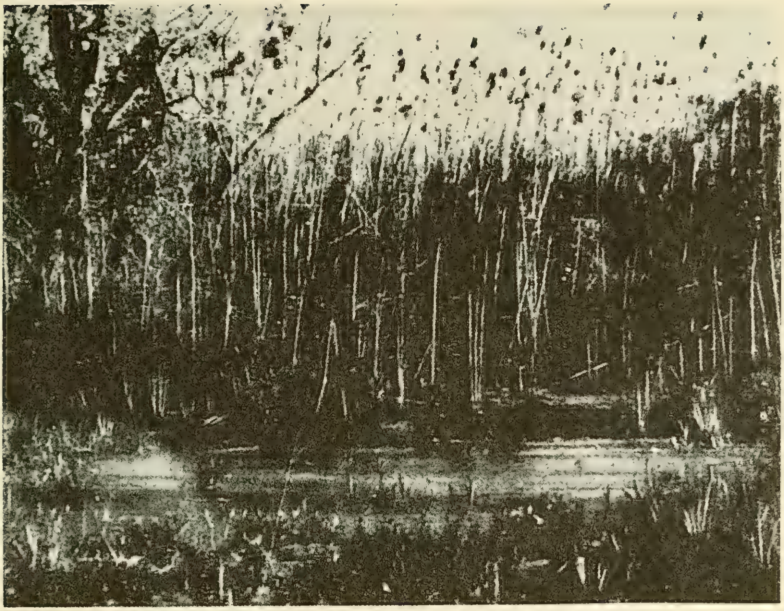


Fig. 12. Reed thickets on the Volga delta, typical habitat of wild boar. Photograph by A.G. Bannikov.

are important locales for wild boar in different periods of the year. Subalpine meadows are visited by boar in summer and the steppe slopes in spring and autumn (Antipin, 1941; Flerov, 1935; Zverev and Keleinikov, 1947; Shul'pin, 1948; Ivanenko, 1956). On the low mountains of the Kazakh hillock zone (Chingistau, Karkaralin hills, and others) wild boar live mainly in marshy valleys overgrown with aspen, birch, rose, etc. at a height of 500 to 800 m (Sludskii, 1956).

In the mountains of the Far East (Sikhote-Alin) the main habitats of wild boar are nutpine groves, hilly mixed forests with Mongolian oak and Korean nutpine, swampy mixed taiga, and coastal oak forests. Now and then, in small numbers, boar invade the subalpine zone with dwarf nutpine. The distribution of the animal varies in different seasons and is particularly dramatic in years of failure of major food crops (Abramov, 1954; Rakov, 1956). In the mountains of
48 Trans-Baikal wild boar are confined to nutpine and shrubs in the river valleys (Kopylov, 1950).

In the plains of the Trans-Caucasus, Kazakhstan, and Middle Asia the main and most important habitats of wild boar are thickets of reed, cattails, and shrubs along river and lake banks. Where large areas of such shrubs are available wild boar generally occupy them year-round.

Dense shrubs along river banks consisting of willows, rose, honeysuckle, oleaster, etc., and especially swampy forests can be considered permanent but secondary habitats of these animals since they primarily seek cover in them. Wild boar also live permanently in marshy birch-aspen forests among strips of pine groves in eastern Kazakhstan. Sand knolls and short, prominent hillocks sporting undershrubs also periodically serve as secondary habitats. In Kazakhstan and Central Asia wild boar also visit saxaul woods and groves of *Nitraria* (Dinnik, 1910; Flerov, 1935; Shul'pin, 1948; Lavrovskii, 1955; Sludskii, 1956). In some regions of Tadzhikistan and Badkhyz (southern Turkmenia) boar are regularly encountered in pistachio groves in winter; in spring they fan out great distances into open desert, feeding on meadow grasses, sedges, and tulips (Heptner, 1956). In every case wild boar periodically feed on cultivated crops, especially when crop failures occur in their natural diet.

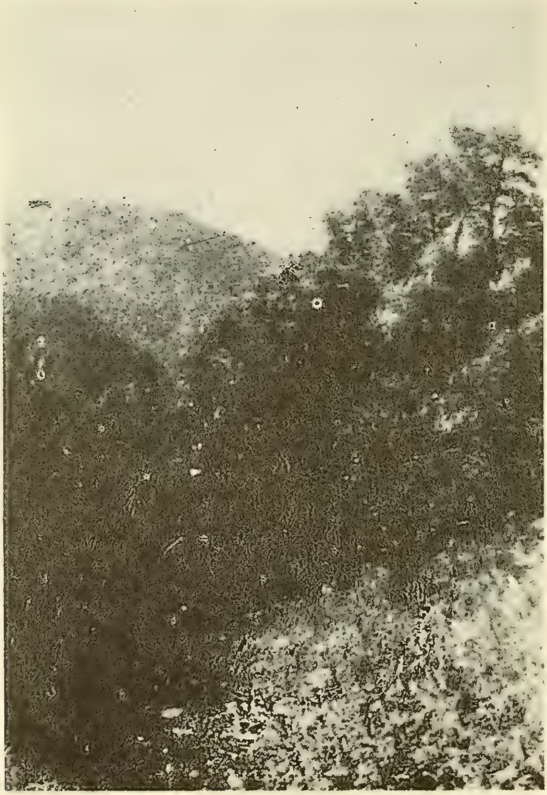


Fig. 13. Birch forest zone in the Caucasian preserve, habitat of wild boar. Photograph by A.G. Bannikov.

49 Fig. 14. Subalpine meadow in the Caucasian preserve. Furrows made by wild boars. Photograph by L.S. Lebedeva.

Food. A comprehensive list of the diet of wild boar would be extremely long and include products of vegetable as well as animal origin. The main items can be divided into four groups: 1) rhizomes, roots, tubers, and bulbs of plants dug up by the animal throughout most of the year and throughout the entire range; 2) products of fruit-bearing trees, nuts, berries, and seeds which the animal eats after ripening, digging them up from under the snow in winter when the crop is abundant; 3) aerial parts of plants; green parts of herbaceous plants are used in the period of their availability, while bark, twigs, and shoots often constitute compulsory food, along with rubbish, in winter; and 4) items of animal origin—earthworms, insects and their larvae, mollusks, fish, rodents, insectivores, bird eggs, lizards, snakes, frogs, carrion, etc.; these serve as food more often in the warm period of the year but also year-round to some extent.

49 Food which wild boar extract from the soil (underground plant parts and animal food) constitutes a greater portion (in terms of quantity) of their diet than food gathered above the soil. In Belovezh Forest boar dig up underground food which in weight is 3.5 times (average) more than that gathered above the soil (Lebedeva, 1956). Digging up the soil to gather food is highly characteristic of wild boar.[30]

[30] The plains of Kazakhstan and eastern Siberia where underground food is less accessible to wild boar in winter because the top soil freezes constitute an exception.

In different parts of an extensive range the diet composition of wild boar differs markedly both in terms of category of food items and its species composition.

In western Europe underground plant foods include roots of bracken (*Pteridium aquilinum*), willow herb, bulbs and roots of meadow herbs, and bulbs of cultivated crops. Wild boar gather this food in early spring and summer and when acorn and beechnut crops fall short, in winter and autumn also (Kissling, 1925; Snethlage, 1934; Oloff, 1951). Acorns, beechnuts, chestnuts, hazel nuts, and more rarely fruits of fruit-bearing trees serve as excellent food. Wild boar invariably prefer beechnuts but acorns, when abundantly available, serve as the most important "fattening" food (Oloff, 1951). A small quantity of the green parts of meadow and marsh grasses and other graminaceous plants is consumed by wild boar in April and May.

Food of animal origin is extremely diverse. It includes earthworms and various insects and their larvae gathered by the animals from the forest bed, including such forest pests as June bugs and pine geometrid moths (Fitingof-Rish, 1952; Klemm, 1944; Khaber, 1950; Tsappe, 1958; Yanda, 1958; and others). In years of abundant availability rodents also constitute a significant food item for wild boar (Oloff, 1951). Other animal foods such as lizards, mollusks, snakes, bird eggs, etc., represent occasional components in the diet of this animal.

The food of wild boar has been studied in detail for the European part of the USSR only in Belovezh Forest (Severtsov and Sablina, 1953; Sablina, 1955; Lebedeva, 1956). The list of wild boar food in
50 Belovezh Forest contains 118 items of plant and animal origin. The underground food (39 plant and 11 animal items[31]) and aerial parts of plants (42 species) are most diverse. Underground plant parts (roots and rhizomes) constitute the most regular food items and are consumed year-round in large quantities. Maximum quantities of root foods are gathered in April (on the average 404 g per 1 m^2) and August (418 g) and minimum amounts in July (237.2 g). In this group of food wood anemone, knotweed, and saltwort [*Polygonatum*] are of utmost importance; in some periods of the year buttercup, calla, dandelion, and bennet play an important role.

Acorns and hazel nuts are occasional foods. This is because years with good yields are few among years when oak and hazel do not bear fruit. Hazel nuts with their poor and rare yield are insignificant

[31] The number of species is more than 39 and 11; root and animal foods are often identified only up to genus.

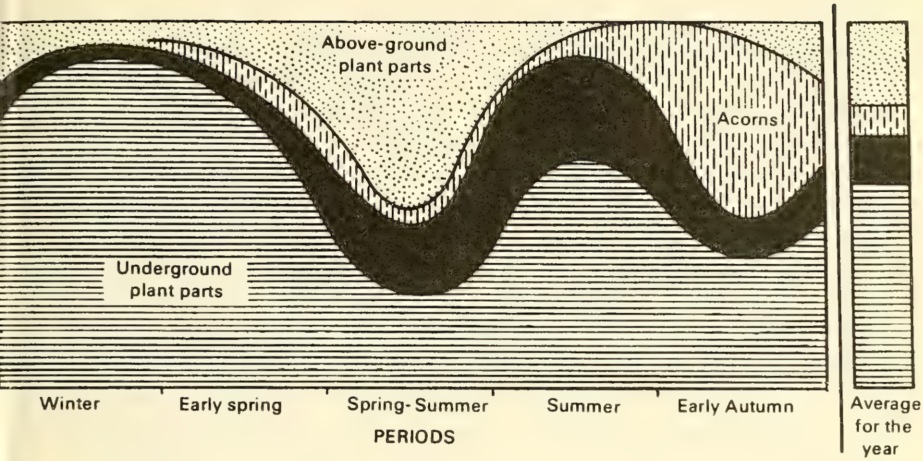


Fig. 15. Variations in food of wild boar in Belovezh Forest around the year (from Lebedeva, 1956).

as food of wild boar. In years of good acorn yields the animal consumes them avidly throughout all of autumn and winter, gathering up to 150 g of acorns from 1 m^2. But since crops of acorn appear only once in three or four years this food is generally not of primary importance to wild boar in Belovezh Forest.

The green parts of plants represent a seasonal food consumed in May to June when wild boar gather an average of up to 119.2 g per 1 m^2. Of the plants from which wild boar eat the green parts five species are primary. Marshy thistle with its large succulent leaves occupies first place, sedge second place (consumed in May when the leaves have not yet become coarse), and nettle, touch-me-not, and bennet come third. The vegetative portions of plants are also consumed by wild boar in winter and horsetail, bilberry, heath, and herbaceous twigs figure prominently. The animal uses these foods intensely in years when the acorn yield is inadequate due to soil freezing.

Among animal foods earthworms are of utmost importance in the diet of Belovezh Forest wild boar. In the total number of cases in which animal foods were recorded earthworms constituted 62%, insect larvae 31.9%, and the remaining 6.1% other types of animals. Quantitatively earthworms represented 74%. Animal components fall in the category of regular food but play a vital role in the warm season of the year when wild boar gather an average of 101 g earthworms from 1 m^2. In the winter, because of their poor accessibility, earthworms are less significant.

Thus in Belovezh Forest wild boar gather much of their food from the soil and forest beds. By overturning the soil with their

muzzle they collect fruits and seeds of trees and shrubs and also the larvae of some insects. Rooting through the soil layers they gather
51 earthworms, larvae of insects, and underground plant parts. Burrowing fairly deep pits in search of food sources they uncover rodents or rootstocks of marsh plants. Boars dig year-round but mostly in winter and early spring when the maximum amount of underground food is utilized. On the average in one year a single boar gathers 1,490.8 g underground food and 452.2 g aerial plant food from 1 m^2 (Lebedeva, 1956).

Apart from the foods mentioned above Belovezh Forest wild boar also consume potatoes, artichoke roots, and cereal crops. However, only part of the population penetrates farms and that, too, mainly in years of failure of forest food crops. Mushrooms and rodents are of minor importance in the food of wild boar (Severtsov and Sablina, 1953; Lebedeva, 1956).

In the montane forests of the Caucasus the main groups of food of wild boar are the same as those in western Europe but their role differs somewhat. The importance of different foods in the Caucasian preserve, based on the frequency of their occurrence in 35 dissected stomachs, is as follows: roots and rhizomes of herbaceous plants (65.7%), beechnuts (62.9%), green parts of herbaceous plants (48.6%), acorns (22.9%), vertebrates (14.3%), earthworms (8.4%), and pears (5.7%); insects, apples, and damson plums were found in an equal number of stomachs (2.9%) (Donaurov and Teplov, 1938).

The underground parts of herbaceous plants represent permanent year-round food of wild boar but do not occupy an important place in their diet. These foods acquire utmost importance at the end of spring and early summer. They become vital in winter in those years when the yield of nuts is unsatisfactory. Otherwise, even rootstock occupies a prominent place in winter in the food of wild boar since the accessibility of fruits and nuts is minimal and their reserves exhausted (Nasimovich, 1939). In the Caucasian preserve the rhizomes, roots, and bulbs of eight species of plants are consumed avidly (Loginov, 1936). Donaurov and Teplov (1938) have listed 28 species of plants whose underground parts are consumed by wild boar. In high mountain meadows alone 23 species have been identified, the rhizomes, roots, and bulbs of which are consumed by these animals (Lebedeva, 1956). Evidently the list is much longer than generally supposed.

The fruits of nut-bearing trees, wherever available in the Caucasus and Trans-Caucasus, represent the most important food item for wild boar during most of the year when their yield is abundant. The fruits of fruit-bearing trees are a seasonal food consumed for two or three months in a year. In June and July cherries ripen and wild boar consume them avidly but their overall importance is only secondary. In August and early September the animals concentrate at places where damson plums fall and feed on them extensively, but only for a short period. Even in September, when the damson plum ripens, wild boar leave these thickets to feed on pears and apples ripening immediately thereafter. Furthermore, acorns drop in mid-September, a favorite food item. In November boar shift to ripening beechnuts and also gather fallen walnuts and chestnuts. Thus the fruits of nut-bearing trees and beechnuts constitute the main food of wild boar from October through March, i.e., for five or six months. In the years of their abundance these foods are well preserved under snow and at places where they have not been consumed in winter serve as an important food in spring, i.e., in March and April. Should wild boar come across them later in the year they will consume them even when they have sprouted.

The green parts of herbaceous plants are of great importance at the end of spring and summer but are utilized in winter as well when wild boar consume a fairly large amount of winter-green plant species. In winters with heavy snows and poor yields from nut-bearing trees the animals consume the bark of trees and fungi (Donaurov and Teplov, 1938).

Among animal foods of utmost importance to wild boar in the Caucasus are earthworms. The animal will root through large areas of meadows in search of them. It consumes a small quantity of
52 insects, rodents, and bird eggs. Carrion is also consumed; under conditions of starvation instances of cannibalism have even been reported. Cultivated plants represent seasonal foods which play an important role only in some regions of the Caucasus and Trans-Caucasus from July to October (Dinnik, 1910; Satunin, 1906; Markov, 1932; Donaurov and Teplov, 1938; and others).

In the forests of the Far East underground parts of plants also constitute a considerable portion of the diet of wild boar throughout the year. They are evidently of great importance in autumn and in the first half of winter, especially in the event of crop failure among nut-bearing trees. The animals dig up the roots and rhizomes of such plants as lespedeza, mountain ash, spirea, rhododendron, etc. In summer wild boar avidly root cow parsnip, angelica, burnet, lily, pea, coltsfoot, and other plants.

Seeds of Korean nutpine and acorns of Mongolian oak are the most important food items. In the season of these crops, commencing from September, wild boar feed on them in nutpine and oak forests until midwinter. When the crop is abundant, they will continue to consume pine seeds and acorns throughout winter and spring right up to June of the following year. At the end of summer berries are consumed (Abramov, 1954; Rakov, 1956).

Among plants from which the aerial parts are consumed by wild boar in the Far East, winter horsetail is of primary importance, especially in river valleys when nut crops are inadequate. In places where horsetail is not available the animals consume twigs, mountain cranberries, and terminal branches of white-barked fir and its needles, especially in the latter half of winter. In spring and early summer the green portions of such plants as nettles and some umbelliferous and Amur vines constitute not less than one-half of all the food of wild boar.

Throughout the warm season of the year foods of animal origin become essential. In summer the animals gather earthworms, mollusks, insects and their larvae, rodents, frogs and their spawn, eggs and nestling of birds on the ground, etc. In coastal regions wild boar sometimes feed on marine animals such as crabs, fish, and carcasses of marine animals. After salmon have completed spawning boar will feed on their carcasses (Siberian salmon, humpback salmon, etc.).

In years of poor nut yields boar visit potato, oat, and maize farms at the end of summer and autumn (V.D. Shamykin; Abramov, 1954; Rakov, 1956).

In the montane taiga of Trans-Baikal and northern Mongolia rhizomes, roots, and bulbs (especially of peonies and lilies) represent the most important food items for wild boar year-round on exposed slopes, glades, and forest edges. The animal avidly seeks out the food caches of voles which contain large amounts of root-stock.

Pine seeds constitute a highly nutritional and valuable food. When the crop is abundant boar wholly survive on these nutritive cones, gathering them in autumn and digging them up from under snow in winter. Unfortunately nutpine yields seeds only once every three or four years and hence the importance of underground plant parts as reserve food is paramount. Pine cones are consumed whole by wild boar and stomach contents have yielded up to 6 to 7 kg of this item alone (Bannikov, 1954).

In the spring with the onset of verdure, boar mainly consume whatever green vegetation abounds. In winter, when verdure is scarce, mushrooms, fungi, twigs, cranberries, and pine needles assume considerable importance.

Among foods of animal origin which boar gather in the warm period of the year, earthworms and rodents play an important role. The latter, i.e., forest and narrow-skulled voles, are found in large numbers in the stomachs of boar in winter (Bannikov, 1954; Kopylov, 1950).

In the mountains of Kazakhstan and Middle Asia underground plant parts represent a constant and essential food for wild boar. In the Trans-Ili Alatau the animals feed on bulbs, rhizomes or roots of geranium, tulip, pea, lady's mantle, dandelion, and onions year-round (24 to 100% of finds). These foods begin to predominate in September and become the main food in winter up through March.
53 On Dzhambul mountain (Bet-pak-dala) even at the end of May boar mainly survive on tulip bulbs and rootstock of Oliver's gentians (Sludskii, 1956). In the Vakhsh range (Tadzhikistan) underground parts of 18 plant species have been found in the stomachs of 93 trapped wild boar. From December through March bulbs and rootstocks greatly predominate in the stomach contents of wild boar; in summer and autumn underground parts of plants are always found in the stomachs but in small quantities (Ivanenko, 1956).

Fruits are important seasonal food of wild boar in most montane regions of Kazakhstan and Middle Asia. On the northern slopes of the Trans-Ili Alatau and Karatau wild boar feed on fallen apples in autumn. Boar of the Talasski Alatau and Pskem and Ugam ranges, as well as in other mountains of Middle Asia, gather fruits of walnuts, damson plums, plums, and pistachios (Sludskii, 1956). On Vakhsh range fruits of damson plums, hawthorn, dog rose, and walnut, pods of flax, and ears of wheat are predominant foods of wild boar in August through September (Ivanenko, 1956). In western Kopet-Dag the usual food comprises pistachios, damson plums, figs, blackberries, almonds, walnuts, pears, and other fruits. In Uzbekistan and Kirgizia almonds, walnuts, pistachios, and grapes are excellent fattening foods (Kashkarov, 1932; Flerov, 1935; and others).

In the Trans-Ili Alatau from the end of April through August the aerial parts of plants, mainly herbage, predominate (40 to 53% of finds). They are also found in small quantities from January to March as well as in September and October (Sludskii, 1956). Parts of 15 plant species have been found in the stomachs of wild boar caught on the Vakhsh range; in April and June boar consume leaves and stalks of grasses along with seeds of leguminous plants (Ivanenko, 1956). Foods of animal origin found in the Trans-Ili Alatau boar comprise larvae of insects, worms, terrestrial mollusks, and rodents. The latter, when prolific in October, constitute an appreciable percentage of boar food (Sludskii, 1956).

On the Volga delta and along other rivers of the Caspian, and rivers and lakes in the plains of Kazakhstan and Middle Asia, the main foods of boar year-round are rootstocks of reeds and cattails. This type of food invariably predominates and its importance drops somewhat only in the period of high floods in May and June, in the event of severe freezing of soil in winter, or for a short period when highly nutritive foods such as fruits of water caltrops or locusts are available. In addition to the above-named primary plants, the underground parts of which are consumed by wild boar, rootstocks of canes, roots of reed grass and sedge, and bulbs of sagittaria are also dug up by the animal. In some places boar avidly dig up roots of licorice, Indian hemp, spurges, thistles, and other plants.

In the deserts between the Caspian Sea and Lake Zaisan in summer, especially from the middle of April to July, ferula roots assume much importance. In search of these roots wild boar leave river catchment areas and wander many kilometers deep into the desert. Sometimes the animals feed on starchy ferula roots in autumn and early winter as well. In deserts boar dig up roots of tiny saltwort and saxaul [*Haloxylon*] (Karelin, 1875; Lavrovskii, 1955; Sludskii, 1956; and others). In the Badkhyz (southern Turkmenia) wild boar enter the open desert from the mountainous parts of the country (Gyaz-Gyadyk) in winter and spring and feed not only on the aerial parts of plants (mainly meadow grass and sandy sedge forming dense thickets in some years), but also on their underground parts and on bulbs of numerous tulips. The latter, evidently, is a favorite food of wild boar (Heptner, 1956).

Fruits and seeds are seasonal foods of wild boar of the desert-steppe regions and important only in some regions. In years when water chestnuts are available wild boar of the Volga delta and Lake Zaisan consume them avidly.[32] Having begun to consume these highly nutritive fruits from August, the animals become extremely
54 fat by the time of freezing weather (Yablonskii, 1875; Lavrovskii, 1955). In the Ili River delta and in several other places in July and August berries (drupes) of *Nitraria* assume great importance and are consumed by wild boar directly from the bush; the animals wade deep into salt marshes for this purpose. At the same time, in tugais, they avidly consume blackberries and, from the beginning of September, oleaster fruits (Sludskii, 1956). In some places they forage in fields of millet, barley, wheat, and also melon fields.

Among plants, the vegetative parts of which play a significant role in the diet of wild boar of this region, reed shoots are important.

---

[32] In China (formerly, probably also in the south of the Soviet Far East) fruits of water chestnuts and the rosettes of lotus with seeds are also important as fattening food for wild boar.

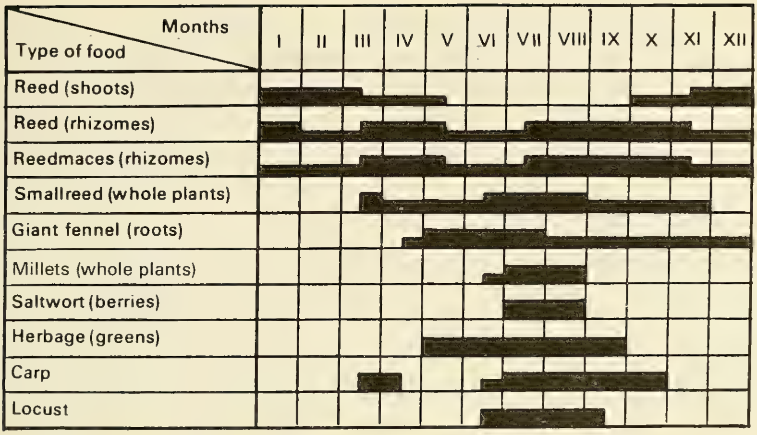


Fig. 16. Seasonal changes in major food objects of wild boar in the lower course of the Ili River (from Sludskii, 1956).

In the event of soil freezing these shoots become the main and often the only food throughout the winter. The green portions of herbage and grasses and racemes of cattail and other plants are of minor importance.

Boar feed on a variety of food. Of the greatest importance is the Asiatic locust. In years of mass proliferation of this insect boar begin to feed on locust nymphs from mid-June; at the end of August they start collecting at places of locust concentrations, and later, until September, move in herds following locusts and consume large numbers of them when they lodge on the stalks of cane and other plants. Up to 1.5 kg of these insects have been found in the stomachs of wild boar. From October right up to the time of soil freezing, and sometimes until spring, wild boar continued to feed on dead locusts or dig up locust eggs. Italian locusts may also serve as an important autumn food (Sludskii, 1956). In northeast Cis-Caucasus (Kizlyar steppe and Caspian reeds) during the mass breeding of locusts in the 1920's, wild boar almost completely changed over to feeding on these insects, and their feces consisted almost entirely of their remains (V.G. Heptner).

In some cases wild boar consume large quantities of fish. In the Volga delta during April and May up to 1.5 kg of vobal [Caspian roach] and carp have been found in the stomachs of wild boar (Lavrovskii, 1955). In several lakes and rivers of Kazakhstan wild boar catch carp in small shoals, open dried-out holes, and during winter freezes (Sludskii, 1956). In the Volga delta the animals regularly forage on fish, vagrant fledglings in colonies of herons and cormorants and fledglings falling from nests. In small ilmens [Volga delta lakes] and kultuks [deeply indented shallow bays] wild boar gather bivalved mollusks, consume trapped muskrats, dig up burrows of mice as well as beetles and their larvae from the sand, destroy accessible bird nests, and consume carrion. On the shallow northwest coasts of the Caspian Sea in the 1920's and 1930's wild boar regularly fed on mollusks at certain places, patiently wading through sea water throughout the night. At the Agrakhan spit, but mainly in Agrakhan Bay, a special method of hunting wild boar on moonlit nights has been developed, taking advantage of this behavior (V.G. Heptner).

55 Living constantly close to water bodies and feeding on succulent diets wild boar always meet their water requirements satisfactorily. They visit water holes and traverse long distances to do so only during winter in the absence of snow.

In some regions, for example the Caucasus, in the warm season of the year wild boar visit saline lakes (Nasimovich, 1938). Such lakes often serve as water holes for wild boar in which they gladly settle down to bathe and gather earthworms. The importance of saline lakes for wild boar and the regime of their visits to them have not yet been studied.

Home range. Herds of wild boar, as well as single animals, are usually confined to permanent sites, the size of the herd depending on availability of food and shelters. Lone animals wander extensively over large areas of the habitat. Swine with small sucklings are confined to a small section. The size of the home range changes with the season. It is most extensive in autumn, especially in the event of nonavailability of normal foods, when wild boar visit farms. In such a case the animals will travel to plantations 6 to 12 km away (Dinnik, 1920; Cherkasov, 1867; Salikhbaev, 1950; Sludskii, 1956). According to Ivanenko (1956) wild boar daily visit feeding grounds located at distances of 16 to 18 km from their lairs, traversing every night distances of not less than 32 to 36 km in a straight line. This information appears dubious. In spring and summer the daily movement of herds of boar usually does not exceed 5 or 6 km as the crow flies. In winter, especially when snow is heavy, boar are confined to small sections of the home range. In Belovezh Forest the area of individual sections of home range of wild boar varies from 0.5 to 2.5 km^2 in winter; the animals daily traverse a few hundred meters to 3 to 4 km (Lebedeva, 1956). In the Far East the extent of daily travel depends on the availability of food and snow conditions and varies from a few hundred meters to 6 to 8 km (Rakov, 1956). In reed thickets along Ili River up to 100 animals were held up in an

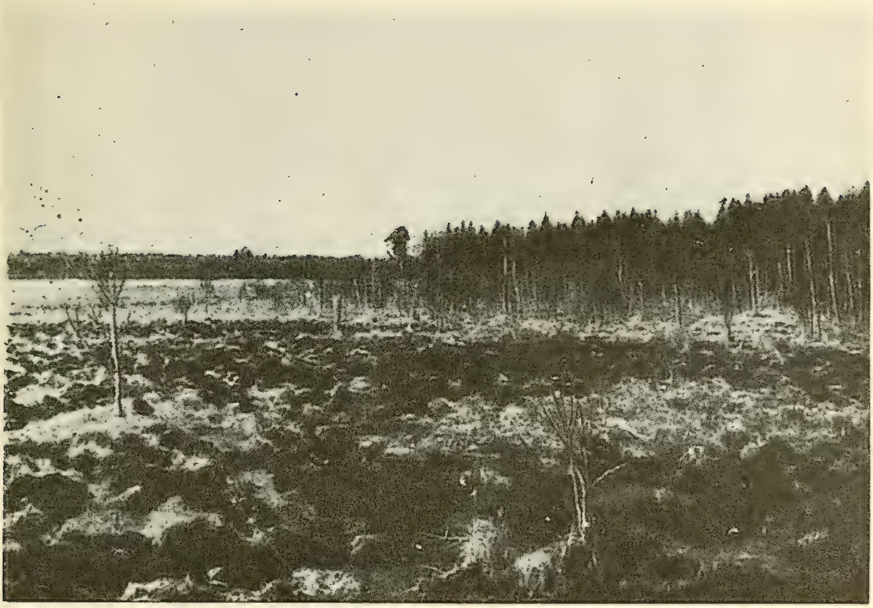


Fig. 17. Furrows made by wild boar in forest clearance in Belovezh Forest. Photograph by L.S. Lebedeva.

area 6.0 km × 3.6 km one winter because of heavy snow. In another case about 50 boar wintered in an area of 300 hectares, while 30 lived in an adjacent section of 120 to 150 hectares (Sludskii, 1956). Only during migration do wild boar traverse 20 to 40 km per day.

56 *Daily activity and behavior.* In summer wild boar set out to feed before sunset and forage until dawn; males go out later than females with sucklings and young. High in the mountains boar are active during the day also. With the onset of cold, in October and November, the period of daily activity gradually shifts to daylight hours. In winter in most regions boar leave their lair in the morning and feed throughout the day; the lower the temperature, the later the departure of the animals for feeding. There are references to wild boar leading a nocturnal way of life even in winter in the southern part of the range. In spring, in April and May sows with sucklings leave the lair only during the day; at this time adults set out to feed in the evening, returning to the lair quite often at midnight and feeding for a second time early in the morning. Wild boar leave the lair invariably in the direction of the prevailing wind or across it and return against it.

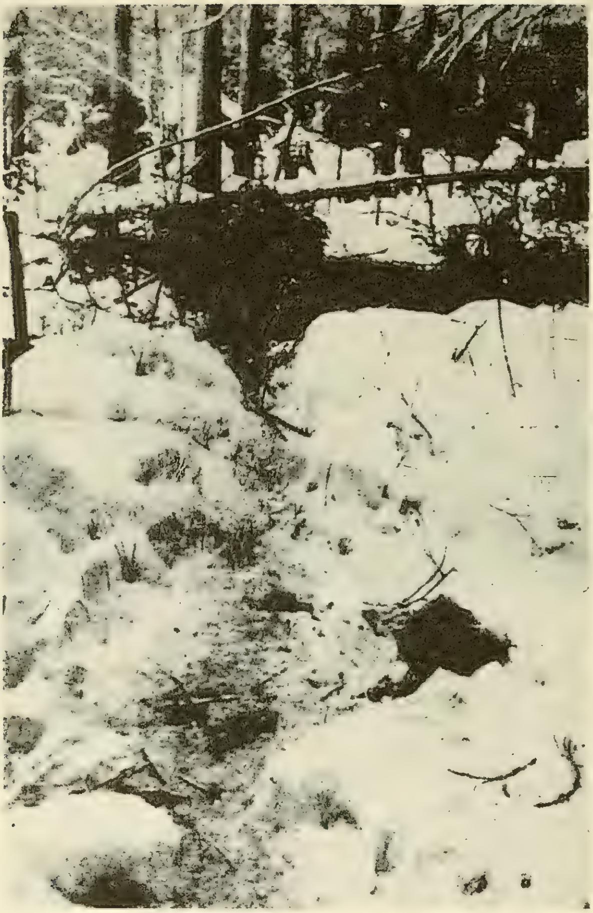


Fig. 18. Spring lair of sows with sucklings and track leading to it. Belovezh Forest. Photograph by L.S. Lebedeva.

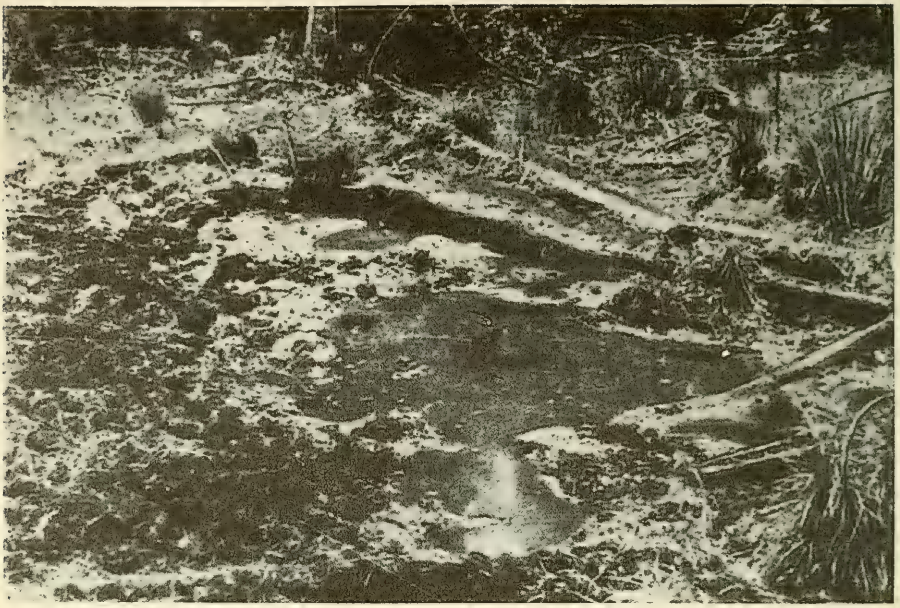
Wild boar make their lairs in one section of the home range. In winter the structure of lairs is more complex than in summer when the animals quite often lie directly on the ground after raking up the soil or stones. In forests boar make lairs more often under the protection of dense tops of trees or in dense undergrowth. Thus in the Caucasian preserve, of the 70 lairs examined, 40 were beside trunks of fir trees (Donaurov and Teplov, 1938); in Belovezh Forest, of 76 lairs, 46 were under spruce and 13 in dense undergrowth (Lebedeva, 1956). In Badkhyz wild boar like to lie under pistachio trees 57 (Heptner, 1956). In mountains in winter the animals usually spend their time on the sun-warmed slopes and in summer among large boulders or under rocks on the steep northern slopes. The winter lair is in the form of a depression among gathered dry twigs, moss, branches, pine needles, etc. In reed thickets the lair is in the form of a large heap of stalks and leaves; the animal either lies on top of the heap or burrows into it. The form and size of the lair varies. Males rest solitarily and their lairs have a thicker bed than those of females and sucklings. The elongated lair of the male corresponds to the body form of the animal using it. Lairs of females and sucklings are often circular. The female and her sucklings frequently rest in the same lair. Group lairs in which up to 10 to 15 animals spend the night are also known. In winter boar often rest under haystacks. The winter abodes of boar in eastern Siberia, Mongolia, Kazakhstan, and the Far East are more complex than those in Europe and the Caucasus. They are made up of large heaps of branches or reeds under cover of which the lair is built with a warm and dry bed of moss or dry twigs. The lair built prior to farrowing in which the litter spends most of at least the first two weeks, usually has a roof of branches of dry grass. Such lairs also have thick walls and a soft bed made of plant material.

In area inhabited by boar there is always a place for wallowing in the form of a depression or pit filled with water and mud. Nearby soil is covered with tracks and adjacent trees, shrubs or rocks splashed with mud and scarred with animal scratchings. If there is a nonfrozen water body available, boar bathe in all seasons of the year, but particularly so in the warm period when there are no rains, in the period of molt, and in the breeding season.

Boar have relatively mobile middle toes and a distinct additional area of support in the form of the rear portion of the sole and hooves of the lateral toes. The weight load on the foot in adults[33] reaches up to 420 to 453 g (Nasimovich, 1955). Wild boar move relatively lightly along marshy, soft ground and shallow snow. However, the short limbs hinder movement in deep snow and the critical height of snow cover is 30 to 40 cm. When the height is more, boar, especially sucklings following their mother, try to walk in single file or use old tracks. At a snow height of over 70 cm adult animals move very slowly, making trenches for themselves (Nasimovich, 1955). Frozen snow crust is fatal to boar, injuring its legs. The wedge-shaped head and anterior body part enable the animal to move rapidly in dense

---

[33] The weight load is 184 g per cm^2 in 1.5-month-old sucklings and 375 g in juveniles six to seven months old. It is less among adult females than in males (Nasimovich, 1955).



58 Fig. 19. Muddy place for wallowing of wild boar in Belovezh Forest. Photograph by L.S. Lebedeva.

reeds and shrub thickets by parting the stalks and branches.

The olfactory sense is extremely well developed in swine and they can smell danger from a few hundred meters upwind; their hearing is also well developed, but their vision relatively weak.

With the exception of adult males and females with small sucklings, wild boar lead a gregarious life year-round; the young follow their mothers usually up to sexual maturity. The adult male tusker, outside the period of rut, is usually solitary and the name "loner" is appropriate. However, adult males have been known to stay with a herd of mothers and young ones during summer.

There are five main factors which determine gregariousness and solitude year-round: 1) isolation of female before farrowing; 2) appearance of offspring and their separation during the course of the year; 3) adult males joining the herd during the breeding season; 4) concentration of animals at places where fattening foods are available; and 5) concentration of animals in the period of abundant snow. The latter two factors are not necessarily annual features and may be absent altogether in some regions.

The herding instinct of wild boar is usually highest at the end of October or November, i.e., in the period of breeding when the males

join the herds of females and young ones. At this time the herd contains up to 5 to 8 adult females, males and 15 to 20 young,
58 making a total of 30 to 40 animals. On the average a herd at this time consists of 6 to 10 animals.[34] At the end of mating, when the males separate from the herd, the herd size drops sharply. From January to March sows and young form groups of 3 to 5 each. In the event of heavy snowfall a concentration of animals occurs, especially toward the end of winter, when collective living facilitates their movement on snow and thus assists weaker animals, particularly the young, to secure food more rapidly. However, large herds are never formed since feeding on a small area would be difficult for a group of more than 8 to 12 animals.

During the brief time of farrowing the herd size shrinks due to the isolation of sows with newborns. But by the end of April or May the herd size increases sharply, reaching in some cases the maximum for the year because of the appearance of the new brood. The previous year's piglets again attach themselves to mothers along with two- or three-week-old sucklings; quite often two or three families merge into a single herd. From June to August families and young usually separate, thus reducing the herd number. At the end of August through September family herds and barren females may combine again at places where nut-bearing trees yield fruit and the herd thus increased once again.

The annual herd number for Kazakhstan wild boar (1,127 animals) averages 5.8 with a maximum of 7.7 and a minimum of 3.9 (Sludskii, 1956). For the Caucasian preserve the corresponding values are 5.9, 10.2 and 3.3 (Donaurov and Teplov, 1938). For Belovezh Forest (17,340 animals) these values are 3.9, 5.2 and 3.0 respectively (Lebedeva, 1956). The mean size of the herd may vary perceptibly in different years and is determined by the total number of animals in the population, the size of the brood, variety and nature of the snow cover, and quantity of food. Thus in Belovezh Forest the average annual herd number over eight years of observa-
59 tion varied from 2.2 to 5.2 (Lebedeva, 1956). For some months, especially in winter and autumn (in subsequent years), instances of seven- to eightfold variations of mean herd size are known.

Seasonal migrations and transgressions. Boar do not characteristically undertake regular seasonal migrations over most of their

---

[34] In the last century when hunting of wild boar in Central Asia was virtually non-existent, herds of boar numbering up to 50 to 100 animals were encountered in the breeding period in the lower course of the Syr-Darya (Skorobogatov, 1924; Sozont'ev, 1925).

60 Fig. 20. Herd of wild boar in Belovezh Forest. Photograph by V. Datskevich.

range. In the plains of Europe, Kazakhstan, and Middle Asia wild boar often live year-round in the same region. However, some change of locality as well as concentration of animals at places where food is abundant probably occurs. The animals may gather in oak groves yielding acorns, leave river floodplains and go to salt marshes for fruits of *Nitraria*, or concentrate in the vicinity of cultivated crops. At the same time, irregular migrations occur fairly frequently and are determined by the failure of the main food sources, high snow cover, soil freezing, and flooding or drying of lakes. In years of total failure of food sources, especially when the soil is covered with ice, migrations of wild boar are known from Belovezh Forest into adjacent regions; such phenomena are also known in Baltic region (Kartsev, 1903 etc., Ling, 1955).

Movement of wild boar from the Volga delta to the Prikumsk valleys downstream, Volzhsk-Ural sands, and Kamysh-Saman lakes have been described (Karelin, 1875; Rukovskii, 1947). Winter migrations are a frequent phenomenon between the Syr-Darya and Amu-Darya when the animals go to the sands of Kyzylkum during intense freezing of the muddy soils of reed clumps. Similar instances of movement of wild boar to a distance of up to 100 to 200 km are known on the Chuya River from where the animals go to Muyunkum, Ili River, and several other regions (Bazhanov, 1945; Shul'pin, 1948; Sludskii, 1956; and others).

In most montane regions wild boar perform regular seasonal vertical migrations associated with seasonal availability of food and nature of snow cover. Wintering wild boar utilize the middle and lower regions of hills but move to the foothills in winters of heavy snow. Boar descend to the middle and lower regions even in autumn when seasonal foods, mostly nuts and fruits, are abundant. In the event of unusual snowfalls in midwinter additional migrations into regions with less snow take place. In April and May a reverse migration occurs. The range of vertical movements varies from a few hundred meters to 1,000 to 1,500 m in the Caucasus, 2,000 m in the Tien Shan, and reaches 60 to 80 km in Sikhote-Alin (Dinnik, 1910; Nasimovich, 1936, 1939 and 1955; Zverev and Keleinikov, 1947; Shul'pin, 1948; Salmin and Shamykin, 1949; Abramov, 1954; Rakov, 1956; Chernyavskaya, 1956; and others).

Reproduction. In most regions mating of wild boar occurs from November to January, but the duration of intense rut in a given year and place usually does not exceed one to one-and-a-half months. In males the commencement of rut is preceded by the development of a "stuffing" ("fat"), in the form of a connective tissue layer of 2 to 3 cm thickness under the skin on both sides of the shoulder blades up to the last rib. These "pads," which begin to grow roughly two months before rut, protect the male from deep wounds which could be inflicted by the tusks of rivals during combat. At the commencement of rut the testes enlarge to almost double their normal size and the glands secrete a viscous, foamy, yellowish liquid, often sprayed on tracks. A male in search of a herd with females in estrus wanders widely and feeds little. On encountering a herd it drives away young piglets and sucklings and starts chasing a female in estrus, often pursuing her in circles. A male on finding a herd with females will vigorously fight any subsequent competitor. At the end of rut males are often severely mauled and emaciated. During rut they lose about 20% of their weight (Markov, 1932). Each adult male generally gathers one to three females, indulging in limited polygamy. The number of females to a male may reach 5 to 8 and, in the period of rut, the herd may number 30 to 40 animals, including sucklings and young pigs (Sludskii, 1956).

60 The period of rut varies insignificantly in relation to the geographic position of the region. Usually rut sets in first in western European animals, at the end of October or early November, and last in Trans-Baikal, at the end of November or in December. Young animals come into rut two or three weeks after older ones. The period of rut may shift sharply to a much later period with a failure in main sources of food. In Belovezh Forest when total failure of food supply occurred, rut was observed only in February and March instead of November and December (Lebedeva, 1956). A delay of one month in

rut in wild boar was recorded around the Ili River as a result of scarcity of food (Sludskii, 1956). Instances have been described (Oloff, 1951) when the mating of wild boar occurred in western Europe in March and April and once even in July and August because of the nonavailability of food.[35]

There are references in literature to extremely well-fed boar also coming into rut late, but more so domestic swine. This phenomenon is probably associated in warm winters in the Caucasus with abundant food supply (Loginov, 1936; Sludskii, 1956). In some cases rut evidently sets in twice, as evidenced by the presence of very small sucklings in January and again in April (Kissling, 1925; Oloff, 1951; Lebedeva, 1956).

Females usually come into estrus for the first time in the second year of life, at the age of 18 to 20 months; males come into rut in the fourth or fifth year of life. However, physiologically females attain sexual maturity in the first year (8 to 10 months) and males in the second year.[36] Males before the age of four or five years are not permitted to mate by the more powerful tuskers. In western Europe only in years of very good availability of food up to 50% of young females take part in reproduction. In years of moderate food supply the corresponding figure is 10%, and in years of poor food supply young females produce no offspring (Oloff, 1951). In Tadzhikistan corpora lutea were detected in some young females, indicating not only their sexual maturity but also their impregnation at the age of 8 to 10 months (Ivanenko, 1956). However, the embryos were usually resorbed as the females at that age were poorly fed. The participation of young females in reproduction under favorable conditions of food supply is also known in other regions.

61 The duration of gestation among wild boar has not been accurately established. In old animals it is 133 to 140 days and in those reproducing for the first time 114 to 130 days (Kissling, 1925; Kenneth, 1943). Mass farrowing occurs from March to May, more often in April. In Europe young usually emerge in March to early April and in Trans-Baikal at the end of April to early May. Corresponding to the change in periods of mating (see above), periods of birth of young also change, being determined by the age of the mother and availability of food.

---

[35] No doubt the situation encountered by Flerov and Gromov (1935) who record February and March as the period of mating and correspondingly May and June as the period of farrow.

[36] Ivanenko (1956), on the basis of a notable enlargement of testes and prostate gland, asserts that males also attain maturity by November or December in the year of their birth (8 to 10 months).

Litter size also depends on the extent to which the female has fed and her age. The litter size of young females is roughly half that of adult females. Depending on the availability of the main sources of food, the number of young in a litter may vary from 2 to 10 or more. On the average swine produce 4 to 6 young. The average number of young in a brood over a 50-year period for western Europe was 5.5 (Oloff, 1951); in Belovezh Forest for 8 years—5.9 (Lebedeva, 1956); Caucasian preserve—4.4 (Donaurov and Teplov, 1938); Far East—6.4 (Salmin and Shamykin, 1949); Volga delta—6.0 (Lavrovskii, 1955); Kazakhstan—5.4 (Sludskii, 1956); northern Mongolia—4.0 (Bannikov, 1954); and Tadzhikistan—3.9 (Ivanenko, 1956). The maximum known number of young in a brood is 10 to 12. Instances have been recorded of a mother with 14 to 16 sucklings but it is highly probable that the offspring of another, dead sow simply attached themselves to a new mother.

The number of fertilized eggs significantly exceeds the number of offspring. In Tadzhikistan 4 to 15 corpora lutea were found in 6 adult females (average 9.6), 2 to 9 embryos in 12 pregnant sows (average 4.3), and 2 to 10 offspring born to 8 females (average 3.9) (Ivanenko, 1956). Hence a large number of embryos are resorbed. Evidently in the years of failure of food sources the number of resorbed embryos increases, which also determines the size of the litter. In western Europe in the years of nonavailability of food the number of young in a brood has averaged 3.0, reaching 8 or 9 in years of plentiful food, with a long-time mean of 5.5 (Oloff, 1951). In Belovezh Forest in years of poor availability of food the average number in a brood has been 3 or 4, reaching 8 to 10 in years of plentiful food, with a long-time mean of 5.9 (Lebedeva, 1956). Such phenomena have also been recorded for the Caucasus, Far East, Kazakhstan, and other regions.

The number of barren females varies even more but precise data are scanty. In Tadzhikistan 5 of 13 dissected females, i.e., about 40%, were barren (Ivanenko, 1956). In the Caucasian preserve on the average 50% were barren (Donaurov and Teplov, 1938). In western Europe over a 50-year period the ratio of fertile to barren females averaged 3:7, i.e., about 60% were barren. In years of abundant supply of food the number of barren females dropped to 25%, while in years with poor food supply it rose to 80% (Oloff, 1951). An increase in percentage of barren females in years of scarcity of food has also been recorded in Kazakhstan, the Far East, and other regions.

Growth, development, and molt. In the first week of birth the young do not leave the lair and, in the absence of their mother, lie closely pressed to each other. Quite often the mother partly covers the litter with bed material before she leaves the lair. Commencing from the second week the young move with the mother, returning to the lair for rest. The young reside in the same lair with the mother up to the age of one year, sometimes more, especially in cold winter. From about the age of two weeks sucklings run away and quickly hide in the grass or stand immobile in dense shrubs or reed thickets when threatened with danger. The stripes on their body, persisting up to July, camouflage them well.

The lactation period lasts from 2.5 to 3.5 months. However, at the age of two or three weeks the young begin to dig up soil, gathering small bits of rootstock and small soil animals. They attempt to dig up soft soil even at the age of one week but evidently do not succeed in gathering food. A small amount of tubers and plant material has been found in the stomachs of two-week-old piglets.

Newborn piglets weigh 600 to 1,000 g; the average weight is 750
62 g. In the lower courses of the Ili River in May sucklings weigh 2.0 to 4.5 kg, in June—3.7 to 9.5 kg, in August—19.5 kg, and in December-January—16 to 30 kg, with an average of 22.5 kg. This is followed by a small drop in weight in February, finally rising to 40 kg toward the end of the first year. The weight of adult females is 65 to 100 kg, average 83 kg, and of males 95 to 200 kg, average 126 kg (Sludskii, 1956). In Tadzhikistan sucklings in summer weigh an average of 16.4 to 17.1 kg, in autumn 31 to 33 kg, and in winter 35 to 38.2 kg. Young pigs weigh 38 to 44 kg. Adult females weigh 71 to 123 kg and males 74 to 144 kg (Ivanenko, 1956). The weight of boar in tugais of Tadzhikistan does not exceed 100 to 120 kg; in the mountains some cases are known of animals weighing 158 kg (Chernysev, 1958). In northern Mongolia (Khentei) the weight of sucklings is 20 to 25 kg by September and of young by spring 27 to 33 kg (Bannikov, 1954). In central Europe the average weight of young pigs of different ages based on long-term data was 19.3 to 28.4 kg, of juveniles 35.9 to 42.8 kg, of adult females 44.6 to 61.4 kg, and of males 54 to 77 kg. The weight of wild boar of all ages varies sharply in different years depending on the availability of food. The maximum weight of boar for different regions in central Europe was 153 to 230 kg (Mager, 1941; Oloff, 1951; and others). In the seventeenth century captured wild boar reportedly weighed 225 to 230 kg (Brandt, 1912). In Latvia the largest animals weigh up to 200 kg but one tusker weighed in at 236 kg (Kalnin'sh, 1950). In Belorussia a male weighing 246 kg was killed in 1951 (Serzhanin, 1955). In the Volga delta in the last century wild boar weighed 48 to 112 kg with a maximum of 190 kg (Yablonskii, 1875). In other regions of the Caspian coast they tipped

the scales at 300 to 320 kg (Karelin, 1875). At present the maximum weight of boars in preserve is 250 to 270 kg (Lavrovskii, 1955).

In Middle Asia (Syr-Darya) in the nineteenth century the maximum weight of males was 128 to 160 kg and very rarely 190 kg (Severtsov, 1874). In the Caucasian preserve the weight of males was 64 to 178 kg with an average of 166 kg; females weighed 48 to 103 kg with an average of 68 kg (Donaurov and Teplov, 1938). At the end of the nineteenth and early in the twentieth century (Dinnik, 1910) males attained weights of 240 to 255 kg and females 120 to 145 kg. In Azerbaidzhan the weight of adult males reaches 142 kg with an average of 114 kg and for young male pigs 68.5 and 63 kg respectively; for adult females these values are 98.5 and 86.5 kg, and for young female pigs 65.6 and 58.5 kg (Safarov, 1958). In eastern Siberia in the last century boar reached 240 to 270 kg (Cherkasov, 1867). In the Far East large boar weighed 150 to 170 kg, some animals weighing up to 300 to 320 kg (Abramov, 1954).

Newborn piglets have one milk incisor and one canine on each half of the jaw. At the age of 2.0 to 2.5 months two premolars appear on each half of the jaw. By autumn, i.e., age six months, all the incisors (3) and premolars (4) have formed. By winter the milk canines and three milk incisors are replaced by permanent teeth; the first molars have also appeared. Yearlings and two-year-olds have only permanent teeth and start developing the second molar. The third (last) molar is seen at the age of two to three years. In the middle of the fourth year all the teeth, except the canines in males, cease to grow, while the first and second molars already have worn-out crowns (Ivanenko, 1955). The growth of canines does not cease in old males and they become very powerful, increasingly curved, acquiring a semicircular form with advancing age.

The life span of wild boar in nature is 10 to 12 years. In western Europe, however, animals older than 6 to 8 years are found very rarely. In Tadzhikistan of the 207 living boar, those older than 6 years constitute only 4.3% (Ivanenko, 1956). References to wild boar living up to 20 years refer to animals living in captivity.

Pigs are born with only bristles; the underfur forms by the age of two weeks. The growth of underfur and the wearing down of ends of embryonic hair (bristles) causes the disappearance of body stripes by the time the piglet is three months old. The maximum growth of hair cover is observed in eight-month-old sucklings.

Wild boar molt for the first time one year after birth, i.e., between
63 March and May.[37] Molt commences with the shedding of underfur;

---

[37] The statement by Sludskii (1956) that young boar molt for the first time at the age of 3.5 to 4.0 months is erroneous.

bristles fall thereafter. New bristles form immediately while the underfur develops only toward the end of July or in August. During June and July only the crown of bristles develops, which explains the silvery-white summer coloration of the animals. By September the hair cover has fully developed (Ivanenko, 1956).

Molt in adult boar proceeds in the same manner as that in young. Well-fed males molt first, followed somewhat later by emaciated animals and lactating females. Molt in the latter may be delayed up to early June. Compared to wild boar of Europe and Middle Asia in eastern Siberia and the mountains molt is somewhat delayed until spring.

Enemies, diseases, parasites, mortality, competitors, and population dynamics. Wolves are the main enemy of wild boar over much of its geographic range. In Belovezh Forest, in spite of its rich ungulate fauna, wild boar are preyed on by wolf more often than any other animal. Remains of boar were found in 24.9% of all the data (1,063) on food of wolves; in various years the percentage ranged from 7.5 to 39.5. In winters of abundant snow wolves inflict the greatest damage on boar (Gavrin and Donaurov, 1954). In the Baltic region the boar population largely depends on the population of wolves, and in severe winters the predators eliminate their prey almost completely (Kalnin'sh, 1950; Ling, 1955). In the Caucasian preserve boar was found in 37.6% stomachs of wolves (154). In winters of heavy snowfall wolves quite often destroy herds of pigs, including sucklings and young pigs (Donaurov and Teplov, 1938). In Kazakhstan (lower courses of the Ili River) boar remains were recorded in 22.3% of all available data (1,052) on food of wolves. One adult wolf can destroy between 50 and 80 boar of different ages in one year (Sludskii, 1956). The significance of wolf as an enemy of wild boar is high in other regions also. Wolves kill mainly sucklings and young pigs, rarely attack sows, and avoid attacking tuskers. Instances are known of the death of predators as a result of injuries inflicted by the tusks of swine. Dense shrubs and cane thickets offer good hiding places for wild boar and hence wolves very rarely attack tuskers or sows.

All the remaining predators are of lesser importance in the destruction of wild boar. In several regions lynx attack piglets and sucklings. In Belovezh Forest boar remains were found in 8.3% stomachs (of 23 examined) and in 3.9% feces (of 206 examined) of lynx (V.F. Gavrin). Instances are known of attacks by lynx on young boar in the Caucasus, Far East, and eastern Siberia (Dinnik, 1914; Abramov, 1954; Cherkasov, 1867). In rare instances sucklings are

64 Fig. 21. Wild boar tracks in mud in reed clumps on Chuya River. Photograph by A.G. Bannikov.

attacked by jungle cats and spotted cats* (Sludskii, 1956). Instances are known of attack of sucklings by snow leopard (Shul'pin, 1948) and leopard (Dinnik, 1914; Bil'kevich, 1924; Baikov, 1927). In the last century in Trans-Caucasus, Kazakhstan, Middle Asia, and the Far East wild boar constituted the main quarry of tiger; however, at present this predator has either disappeared or become extremely rare and hence its role in the destruction of wild boar is minimal. In the Far East brown bear and yellow-throated marten sometimes attack piglets and sucklings (Abramov, 1954). Evidently bear and fox feed on the carcasses of dead animals; it is possible that bear attacks on living animals are exceptional. Instances of killing of sucklings by stray dogs are reported quite often.

---

*Species referred to by this common name is unclear—Sci. Ed.

About 20 species of parasitic worms have been identified for wild boar (Badanin, 1931; Pavlovskii, 1946; Dubinin, 1952; Rukhlyadev, 1952). Maximum infection is observed in summer. The most dangerous helminths are *Metastrongylus* parasitizing the lungs and causing mortality among sucklings. *Metastrongylus* infections occur through an intermediate host, the earthworm. Of pathological importance to wild boar is the fluke *Gasterodiscoides hominis,* which also parasitizes man. Wild boar are likewise known to harbor *Trichinella spiralis* and instances have been described of infection of man by this parasite through the consumption of meat of wild boar (Chun-Syun, 1958). *Taenia solium* and *Balantidium coli* are also known to parasitize wild boar (Appasov, 1958).

Ticks (*Dermacentor, Rhipicephalus,* and *Hyalomma*) and a spe-
64 cies of hog louse (*Haematopinus sus*) parasitize wild boar quite often, especially in the southern regions (Pomerantsev, 1946; Pavlovskii, 1946). The animals also suffer acutely from blood-sucking Diptera. To escape dipteran attacks wild boar spend considerable time in water, move from reed beds into the steppes, hide in dense shrubs, and so on.

Swine plague spreads faster than any other disease of wild boar and causes extensive mortality. Epizootic diseases are well known in Germany, Poland, Hungary, Belorussia, the Caucasus, the Far East, Kazakhstan, and other regions (Kissling, 1925; Kartsev, 1903; Donaurov and Teplov, 1938; Smirnov, 1928; Abramov, 1954; Kovach, 1957; Momberg, 1954; Sludskii, 1956; and others). The extremely contagious foot-and-mouth disease, known among wild boar of western Europe, the Caucasus, and Kazakhstan can assume an extensive epidemic character (Dinnik, 1910; Gutira and Marek, 1931; Sludskii, 1956). Pasteurellosis or hemorrhagic septicemia (Smirnov, 1928) and tularemia are rare; wild boar contract tularemia either from rodents or through blood-sucking insects (Pashova, 1950). Siberian ulcers are also very rare (Andreev and Andreev, 1948). Swine erysipelas is contracted by wild boar from rodents or through hog lice or ticks (Smirnov, 1928). Wild boar also harbor pyroplasmosis and Aujezsky's disease (Skomorokhov, 1951; Andreev, 1948). In Czechoslovakia in 1950; and in Poland in 1954, wild boar suffered from epidemic viral teschen disease (porcine enteroviral disease) (Shaflyarskii, 1955).

In years of abundant availability of food wild boar have no serious competitors in much of their geographic range. In years of poor availability of acorns in mixed forests in the northern part of the range a large number of animals such as deer, squirrels, jays, etc. compete with boar for acorns. In eastern Siberia a similar phenomenon occurs with regard to pinenuts. In the Caucasus squirrels, after their acclimatization, began destroying beechnuts which had not yet fallen. By consuming an appreciable part of the crop they became an acute competitor of wild boar.

Twice within a decade a large number of wild boar died in the Volga delta during floods when the animals became emaciated for want of adequate food and remained in water for many days (Dyunin, 1926; Isakov, 1951; and others). The young particularly die in large numbers in swollen waters due to spring—summer floods in this region, causing a sharp reduction in wild boar population (Lavrovskii, 1955). Such phenomena have been observed in the lower course of the Syr-Darya River (Sludskii, 1956) and rarely in other rivers.

Fires lead to the death of wild boar in Middle Asia, Kazakhstan, and along the Caspian coast. During fires in cane and tugai thickets, especially with strong winds, a significant number of sucklings perish. Furthermore, fires deprive the animals of shelters, making them more vulnerable to wolves (Sludskii, 1956).

65 The population dynamics of wild boar are characterized by sharp numerical changes over short intervals of time. Inadequate food supply combined with deep snow or ice-crusted ground exert a permanent influence on population attrition. The activity of wolves is important everywhere. Years of epidemics and natural calamities (floods and fires) often lead to the death of an appreciable percentage of local populations. Most often mortality of wild boar is the result of a combination of unfavorable factors. For example, in the Polish part of Belovezh Forest over 60% wild boar perished in the winter of 1955 to 1956; the surviving swine were so emaciated that they could not breed in spring. The causes of death were soil freezing, formation of three-layered frozen snow crust, and a high snow cover, all of which prevented the animals from getting at their food. Moreover, rodents depleted the small yield of acorns. In this winter swine erysipelas, which usually affects them lightly, led to the death of wild boar already weakened by inadequate food (Tsabon', 1958).

A rapid increase in population is assured by the high fertility potential of wild boar, large-sized litters, and the early onset of sexual maturity. However, litter size, the age at which females reproduce for the first time, and the percentage of females participating in reproduction vary sharply, depending on the state of the food base (see above). A population of wild boar can dwindle to one-tenth or double or treble in just a few years.

Precise data on the mortality of young swine are scanty. In Belovezh Forest an average of 64% survive to their first birthday (Lebed-

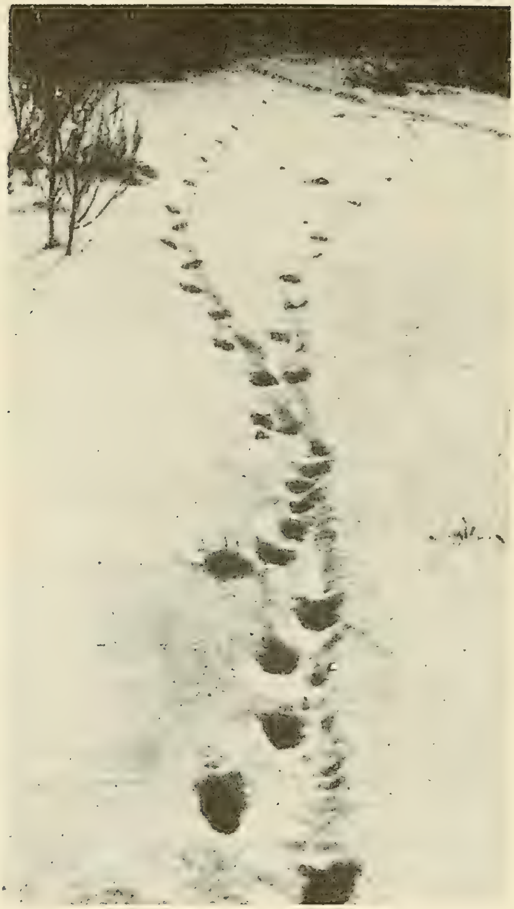


Fig. 22. Tracks of wild boar in snow in Belovezh Forest. Photograph by A.G. Bannikov.

eva, 1956); this figure in the lower course of the Ili is 60% (Sludskii, 1956), and in Khentei about 40% (Bannikov, 1954). When food is abundantly and readily available mortality of young is low and over 90% survive up to the age of sucklings. Contrarily, in years of inadequate food supply, especially when combined with heavy snows and soil freezing, not more than 20% survive to spring. Evidently everywhere the maximum death of sucklings occurs in late autumn and early winter and is determined by worsening conditions of food accessibility, especially during intense frosts. In summer, when sucklings take over feeding themselves, become more mobile, and often run about independently, a second peak of mortality has been recorded (Danaurov and Teplov, 1938; Lebedeva, 1956).

Among adult wild boar the sex ratio is close to 1:1 in most regions. However, among newborns females predominate and constitute 60 to 70% of total births. This reveals a high mortality of females at an early age.

66 The age structure of the herd changes perceptibly in different years. Usually, the year's brood form 50 to 60% and sucklings 9 to 12%. Following severe winters, when sucklings are the first to die and females give birth to small-sized litters, the percentage of piglets and sucklings decreases three or four times compared to the average, and hence piglets and sucklings together form only 5 to 10% of the herd. Contrarily, after a favorable winter the herd acquires a perceptibly youthful appearance.

Field characteristics. Coloration is extremely variable but from a distance wild boar often appear almost black; in summer the bristles gleam in the sun and light, sandy-colored specimens are seen.

Hoofprints of adult wild boar in soil invariably show the imprint of the lateral digits; in small sucklings traces of only two digits are left. The print length of an adult boar ranges from 16 to 25 cm, generally about 20 cm; the width is even more variable but more often about 18 cm (maximum distance between lateral digits). The winter prints are deep. The animals drag their legs and often plough a continuous furrow in the snow. Lone males on selecting a site for lying up turn around, executing a semicircle, and lie down with their head in the direction of the track at the point of entry; females do not turn around in such a manner but lie down straight on the track. Wild boar often lie down at the foot of trunks of densely leaved trees, below upturned trees, in dense undergrowths, shrubs, and in breaks in cane groves after making a suitable bed (see above). The animals make deep tracks leading to places of feeding and wallowing (see above). The habitat of wild boar is characterized by deep furrows in the soil of meadows, forests, or cane thickets, ploughed to a depth of 10 to 20 cm. The feces of wild boar in autumn, winter, and most of the summer are in the form of three or four flat cakes, 2.0 to 2.5 cm in diameter, joined together; of these one is larger (thicker) than the rest. In spring and early summer feces often lack definite form.

While resting adult males are silent, females grunt often, and piglets whine. A frightened boar makes a loud noise ("ukh! ukh!") or emits a screech ("gu-gu-gu!"). While feeding boar wave their tail rhythmically. On sensing danger the tail hangs down or rises in the form of a question mark, the animal stops feeding, and raising its

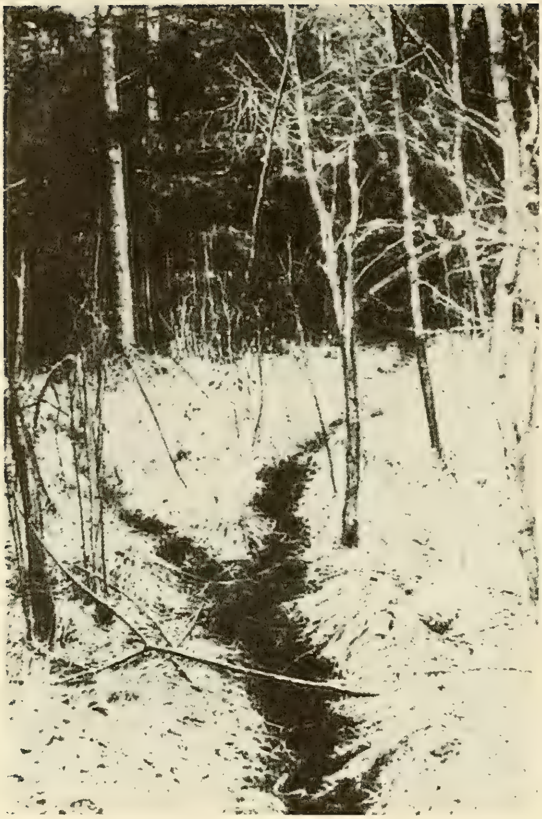


Fig. 23. Tracks of female wild boar with brood in Belovezh Forest. Photograph by L.S. Lebedeva.

snout gulps air which gives rise to an audible puffing sound. (A.B.)

Economic Importance

The extent of catch of wild boar in the past and at present in the Soviet Union is difficult to assess since the main part of the catch is retained by hunters. In pre-Revolutionary Russia about 50,000 animals were caught, mainly in the Caucasus, along the Caspian coast, and in the southern part of the Far East. In Middle Asia wild
67 boar was caught less as its meat was not used for food; rather it was killed to protect melon fields and plantations.

At present about 7,000 to 8,000 swine are caught annually in the Caucasus (Vereshchagin, 1947), 6,000 to 7,000 in Kazakhstan (Sludskii, 1956), and about 5,000 in Middle Asia. No information is available for other regions but evidently the total for the country as a whole is currently between 60,000 and 70,000 per year. Data per unit of land are not available. In Germany at the end of the nineteenth century 0.08 to 0.1 animals were caught per 100 hectares. At the end of the 1930's this figure had risen to 0.21 to 0.26. Between 1935 and 1939 a total of 33,000 animals were caught (Oloff, 1951).

In the past the main methods of catching were extensive "beats" and hunting with dogs. Beats were done on foot as well as on horseback. Beaters moved in a chain or rode through the forest or cane thicket driving the animals toward a group of hunters. In the desert-steppe regions thickets were often set on fire. Setting fires for the purpose of hunting is now prohibited. During the hunt the animals were killed with lances and spears; shooting came later.

Hunting with dogs, when a large pack of up to 20 or more strong freely scoured cane thickets and forests, was extensively practiced earlier; now dog packs are prohibited. In earlier days a large number of piglets and sucklings were frightened by the dogs and killed. In hunting with a pair of dogs, they are set only on the trail of an adult animal. The task of the dogs is to stop the boar and hold it at bay until the hunter arrives. Also prohibited now are methods using traps, loops, crossbows, and pit traps. At present hunting on the sly is commonly practiced everywhere. The hunter follows a fresh track and, orienting himself by sounds, approaches the boar against the wind. It is extremely difficult to approach a silent and wary solitary male. Hunting by lying in wait is also practiced equally extensively. At the feeding grounds of wild boar, often in plantations, groves, and other places, pits are dug, hides set up, scaffolds constructed on trees, etc. where the hunter waits for the animal, taking advantage of the prevailing wind direction. This type of hunting is sometimes combined with beats.

At present the period of hunting in most regions extends from September 1 through December 1. The period from September 15 through November 15, i.e., after the cessation of lactation and before some of the females become pregnant again, is a more correct time.

Meat, hide, and bristles are the products obtained from wild boar. The weight of meat in summer amounts to 55% and in winter 65% of body weight. According to meat-dressing organizations the body of a boar should yield an average of 50 kg meat. A large boar may yield 15 to 20 kg fat and, exceptionally, even up to 30 kg or more. The hide of a large boar can stretch up to 300 dm^2; it yields 350 to 1,000 g bristles and about 400 g of "fuzz"

When wild boar live in the neighborhood of townships, gardens, and farms, they cause damage by digging up potatoes, damaging melons, watermelons, and maize, eating the crop from the stage of milk formation onwards. In the latter case damage is due mainly to trampling considerable areas in plantations (Kartsev, 1903; Satunin, 1906; Shillinger, 1928; Markov, 1934; Kalnin'sh, 1950; Abramov, 1954; Sludskii, 1956; Kissling, 1925; Snethlage, 1949; and others). However, the damage inflicted by wild boar is often exaggerated (Kissling, 1925; Ling, 1955). Only in small sections of farms situated among forests or cane thickets, when the wild boar population is high, do the animals inflict significant damage on cultivated plants. The extent of availability of natural foods is of great importance; when natural food is not available, boar enter farms in large numbers and damage is severe. In Belovezh Forest in years of moderate availability of natural foods 34 to 47% of the population enter farms. In clearings animals damage potato and buckwheat crops up to 30%, but on the whole the damage to fields is 0.08 to 4.7% (Lebedeva, 1956). To protect farms from wild boar, in Central Europe several measures have been suggested, including distraction and fright (Snethlage, 1949). In Kazakhstan leashing dogs to long chains at places where boar enter the plantation has been suggested as the most effective method of protection (Sludskii, 1956).

68 Wild boar play a significant role in afforestation but this aspect has not been studied adequately. The number of seeds which a swine consumes in years of moderate availability does not delay seeding of a forest and the damage inflicted by wild boar in this process is imperceptible (Oloff, 1951). The digging activity of boar is very important to the life of a forest. By digging up large areas the animals promote the sowing of seeds which, in turn, leads to restoration of wood-forming species. The role played by wild boar is very important therefore in the case of mossy fir stands of the Tien Shan (Korelov, 1947), nutpine groves of eastern Siberia (Abramov, 1954), and oak forests of Europe (Snethlage, 1949; Lebedeva, 1956). The extremely positive role of wild boar in afforestation is evident when their population is not high. However, in the event of too high a density they plough up the same section over and over and dig up the germinating seeds. They also promote a shift in wood-forming species, as observed in Central Europe where oak forests were transformed into birch due to their activity (Fitingof-Rish, 1952). In Belovezh Forest wild boar promote the replacement of oak by spruce (Lebedeva, 1956).

The importance of wild boar in the destruction of forest pests has been well known in western Europe for a very long time (Hennert, 1797; Spangenberg, 1818; Ratzburg, 1856; Fohlisch, 1880; Meimaiter, 1915; Gaber, 1950; Klemm, 1951; and others). The importance of wild boar is particularly notable in the destruction of larvae of June bugs and *Cephalis obitis;* the animals reduce these populations by 20 to 30% (Fitingof-Rish, 1952). Boar also destroy the pine geometrid moth and other forest enemies. When there are local spurts in population of forest pests, wild boar suppress them and prevent their outbreaks. However, if an outbreak has already occurred in a large area, wild boar are unable to restrict its further spread (Tsappe, 1958). There are no concrete data to demonstrate the importance of wild boar in the destruction of forest enemies within the Soviet Union.

At the end of the last and the commencement of the present century small groups of wild boar were released time and again in private farms around Moscow. Experiments with acclimatization were carried out in 1937 in Zavidov hunting area, north of Moscow, by releasing nine boars. In 1940 there were about 100 of them and by 1947 their number exceeded 300. The animals had dispersed widely and were found at places tens of kilometers away from their place of release. Hence only some of them visited the original feeding points (I. Lyapunov). Between 1948 and 1949 in the hunting zone of Ryazan' district 40 boar were released. They prospered and dispersed into neighboring districts; some animals moved 60 to 180 km from the point of release but evidently all of these died. Wild boar were released in small numbers in the 1940's and 1950's in other farms of Moscow, Yaroslav, and adjoining districts. In 1957 a total of 35 Far East wild boar were released in the Crimean hunting preserve (Tkachenko, 1959). In the warm season wild boar find adequate natural food everywhere, but in winter are compelled to supplement this food, the extent of which is determined by the amount of natural foods available and their accessibility (height of snow cover and soil freezing). Even when food supplements to boar were stopped, the animals were still found six years later but subsequently disappeared. In addition to supplying food supplements, extensive protection of wild boar farms from wolves is essential. The permissible density of wild boar in mixed forests in European sectors is 6 to 12 animals per 1,000 hectares. In farms where muskrats are present, wild boar destroy their burrows and feeding places in winters of ice crusts and hollow ice (Pokrovskii, 1950; Novikov, 1957).

In captivity wild boar get on well but young sucklings without a mother grow slowly and poorly. Wild boar interbreed readily with domestic swine; in nature interbreeding is known in the Caucasus, Belovezh Forest, the Far East, and other regions. Hybridization experiments with large white swine and wild boar in Kazakhstan established that the resultant hybrids possess high vitality. Hybrids of the third generation feed on less concentrated types of food, record very high (by 14 to 15%) weight increase, and consume less food per kg weight increase. Their skeletons are fattier than those of the large white variety. Hybrid swine adapt well to the utilization of summer pastures in southeast Kazakhstan (Butarin, Es'kov, Miletskii and Bagrovskaya, 1955). (A.B.)

Suborder TYLOPODA Illiger, 1811

69 Tylopoda are artiodactyls of large to moderate size with relatively elongated limbs and either of heavy or light build.[1]

These animals walk on the two toes present on each leg. The lateral toes are totally reduced and the metacarpal or metatarsal elements totally absent. The remaining corresponding bones of the toes fuse into a cannon bone, which is bifurcate at the end and has no paired blocklike articulating surface. Terminal phalanges small and rounded. Hooves absent, replaced with only small, blunt, curved nails. Undersurface of foot consists of a broad, paired or unpaired, elastic, callused, cushionlike padding. Ulna and radius fuse in the proximal and, in some species, even in the distal part; fibula partly reduced.

Skull with an extremely elongated frontal portion. Orbit closed from behind. Ethmoid pit well-developed. Tympanic bulla with lamellar osteosepta. Sagittal crest present. Horns absent and mastoid bone exposed. Condyle of lower jaw spherical.

Young camels have three upper incisors on each side, while adults have only one canine-like upper incisor on each side. Lower incisors total three, the third in some animals also resembling a canine. Canines typical in form (conical), present in both jaws, and separated by a diastema from premolars. Lower canine separated from incisors. First premolar in upper jaw has the form of a canine in some camels and is separated by a diastema from molars. Latter with crescent-shaped cusps (selenodont) and hypsodont. Dental formula:

$$\mathrm{i}\ \frac{1}{3},\ \mathrm{c}\ \frac{1}{1},\quad \mathrm{pm}\ \frac{2\text{–}3}{2},\quad \mathrm{m}\ \frac{3}{3}\ = 34 \text{ to } 32.$$

Abdomen greatly stretched at the groins and most of the thigh free. Upper lip highly cleft and serves as a prehensile organ. Stomach complex ("ruminant") and consists of four chambers, but differs somewhat compared to the stomach of true ruminants (the third chamber is not distinct while the first is designed to store water).

[1] As this suborder is not found wild in the Soviet Union, its characteristics are very briefly summarized. It is possible that the modern species of wild camel (*Camelus bactrianus,* not as widespread as the Pleistocene *Camelus knoblochi*) survived in Central Asia and Kazakhstan until recent times. It is known from the kitchen-refuse of the Andronov civilization (1,000 to 1,500 B.C.; Vereshchagin, 1956).

Chewing the cud is characteristic. Cecum short. Skin glands few (occipital glands). Hair cover normal, well developed, sometimes even extremely well developed. Functional teats two and inguinal in
70 position. Preputial orifice set far behind and turned backward. Placenta diffuse. In two species one or two large humps occur on the back. Red corpuscles oval (the only case among mammals). Sex- and age-related changes absent.

These are desert, steppe, and mountain animals; they form herds and are strictly herbivorous.

As wild animals they are distributed in Central Asia and South America; the domesticated form is found in the arid zones of Asia and North Africa (camels), and South America.

Tylopoda are a very distinct group with several primitive characteristics and some specialized and progressive characteristics. They became isolated in the Middle Eocene and the present-day family of camels (Camelidae) has existed from the Upper Eocene onwards. Of the several subfamilies and genera, only one subfamily (Camelinae) with two genera, the true camel (*Camelus* L., 1758) and llama (*Lama* Fisch., 1775), has survived to date.

The suborder has four living species: the two-humped camel (*Camelus bactrianus* L.) well known in the wild state in the deserts of Central Asia (almost exterminated at present), the one-humped camel (*Camelus dromedarius* L.), the guanaco (*Lama guanicoë* Mill.), and the vicuña (*L. vicugna* Mol.) inhabiting South America.

The one-humped camel was never known in a wild state even in historic times. Only feral camels existed in North Africa. According to one view the one-humped camel is not a distinct species but only a domesticated, more civilized form of the two-humped animal. Both forms interbreed freely. In the embryonic stage the one-humped camel has two humps. At the same time fossils of one-humped camels are known from the Tertiary formations of North Africa and used to live in a domesticated state with inhabitants of the Sahara even in the Stone Age.

The two-humped camel is a domesticated animal in Central Asia and Kazakhstan, while the one-humped animal is known in North Africa, Asia, Turkestan, Australia, and to some extent North America. The llama (*Lama glama* L.) is a domestic form of guanaco, while the alpaca (*Lama pacos* L.) is a domestic form of vicuña.

Feral one-humped camels are found in the estuary of Guadalquiver [Spain] (?) and in the United States (Texas, Arizona, and New Mexico).* (V.H.)

---

*No longer present in the United States—Sci. Ed.

Suborder RUMINANTIA Scopoli, 1777

71 Ruminantia are specialized artiodactyls of small, medium, or large size, with relatively long limbs, and mostly of light and slender build.

These animals are hooved, with four or two digits and typical hooves. Lateral digits, if present, rudimentary and, in most cases, do not reach the ground and are nonfunctional. With few exceptions (Tragulidae), metatarsal and metacarpal bones of lateral digits either rudimentary and do not articulate with the tarsal and carpal regions, or completely absent. With one exception,[1] typical cannon bone present with two parallel, blocklike articular surfaces at the distal end. Carpal and tarsal bones fuse to some extent (at least the cuboid and naviculare are invariably fused). Ulna invariably reduced, set behind radius and in contact with it, or sometimes the two bones fuse; exceptionally (Tragulidae) ulna fully developed and separate. Shaft of fibula reduced (only the rod-shaped central portion sometimes preserved) and only the rudiments of its proximal and distal ends present (it forms an independent bone, os malleolare). As an exception, in Tragulidae, shaft of fibula complete. Transverse processes of cervical vertebrae pierced by vertebrarterial canals (art. vertebralis).

Skull with greatly or moderately elongated facial part except in diminutive species; considerable development of cranial region ("infantilism" in diminutive species). Longitudinal axis of skull usually highly flexed. Orbit closed from behind. Ethmoid pit well developed. Tympanic bulla tubular; exceptionally (Tragulidae) with lamellar osteosepta. Sagittal crest absent. Horns (several types) usually present at least in the male but often in both sexes; absent in a small number of species. Condyle of lower jaw elongated transversely (permitting lateral movements of lower jaw while ruminating).

Upper incisors absent. Horny plate occurs on the lower surface of the anterior part of premaxillae. Upper canine absent in most species but present in some (in hornless forms—Tragulidae and some Cervidae) where it is highly developed in males. First upper

---

[1] *Hyemoschus* (Tragulidae). Even in this species partial or total fusion of the metatarsals takes place in old age. The progressive specialization of limbs in artiodactyls generally occurs first and more intensely in the hind limbs which, evidently, is associated with their more dominant role in locomotion compared to the forelimbs.

premolar normal (does not have the form of a canine) and not separ-
72 ated by a diastema from row of cheek teeth. Lower incisors flat and
broad (spatulate). Lower canine in contact with incisors and very
similar in form. Cheek teeth cusps crescent-shaped (selenodont);
curvatures of crescents in upper and lower jaws set opposite to each
other. Molars and premolars hypsodont to various degrees, usually
with late closing roots and sometimes passing into prismatic type
(Tragulidae and Cervidae), and brachyodont. General dental
formula:

$$i\,\frac{0}{3},\quad c\,\frac{0-1}{1},\quad pm\,\frac{3}{3},\quad m\,\frac{3}{3} = 34 \text{ to } 32.$$

Stomach complex ("ruminant") with four well-developed sections, three as an exception ("third stomach" rudimentary) in Tragulidae. Rumination of regurgitated food and marked participation of bacteria and protozoa in digestive process are characteristic features. Large cecum invariably present. In most species integumentary glands well developed on head (facial and occipital), legs (carpal, tarsal, and metatarsal), inguinal region, and some other parts. As an exception (Tragulidae), integumentary glands (at least facial, tarsal, and metatarsal) absent. Hair coat normal (bristles absent) but partly reduced in some cases. Teats inguinal and two or four in number. Sexual dimorphism usually well manifested, sometimes very sharply, and occasionally indistinct. Age related changes sharp in some but relatively weakly manifested in most. Placenta cotyledonary; diffuse as an exception in Tragulidae.

Ruminants are an extremely diverse group of artiodactyls. They include animals varying widely in size, external appearance, and biology such as mouse-deer, musk deer, deer, giraffe, ox, goat, sheep, and diverse varieties of antelope. The largest of these forms, the giraffe (see characteristics of the order), attains a weight of 1,200 kg and the smallest weighs 2 to 3 kg.

With few exceptions (ox), ruminants are slender and mobile animals capable of sustained fast running (fastest of all nonflying mammals); some are adapted to climbing rocks. They inhabit extremely diverse biotopes, from tundras to tropical forests and marshes, most of which are associated with open biotopes (steppes and steppelike zones and mountains); a few are confined to forests and marshes or dense grassy thickets (similar to hares). These animals live in herds to some extent, except Tragulidae which live singly. They give birth to one or two offspring; four to seven are exceptional (*Hydropotes*). They are herbivorous and feed mainly on grassy vegetation.

Ruminants are a very widely distributed group of the order, inhabiting all of its geographic range except Tierra del Fuego, Madagascar, and the West Indies. The southeastern boundary of their range extends along the island region between Asia and Australia and includes the islands of Timor, Ceram, Buru, Halmahera (Dzhilolo), and the entire group of Moluccas and the Philippines. Ruminants are absent in Tanimbar, Kai, Aru, and New Guinea if sambar, acclimatized there, are not taken into consideration. Several species (deer, tahr, chamois, and others) have been acclimatized in New Zealand.

In diversity of adaptation, biological types, distribution, number of species, and numerical strength Ruminantia are an extremely flourishing extant group of artiodactyls and of hoofed animals in general. Although in some morphological features they are no more specialized (often less) than Tylopoda, on the whole (biologically) they represent a most progressive branch of the order.

Present-day ruminants, in spite of their varied diversity, are extremely distinctive and sharply delineated from suborder Suiformes.

The differences between suborders Tylopoda and Ruminantia are less striking. This has prompted some zoologists to combine these two groups into a common suborder, which is hardly justifiable. Both groups possess important differences; they flourished inde-
74 pendently from the Eocene period (appearing at the commencement of evolution of the order). The most striking similarities between Tylopoda and Ruminantia (complex stomach, some structural features of limbs, etc.) are largely the consequence of their parallel adaptation. There are no "connecting links" whatsoever between the two groups. Nevertheless, Ruminantia are closer to Tylopoda than to Suiformes.

In basic structural plan the suborder represents an extremely homogeneous group. As can be seen from the morphological characteristics given above, only the mouse-deer (Tragulidae) with its several primitive features stands out prominently in the suborder.[2]

The ruminant group Tragulina appears in the Upper Eocene

---

[2] Some specialists in taxonomy are inclined to separate them from the remaining ruminants, i.e., not only typical ruminants (Pecora, i.e., Ruminantia without Tragulina) but also Tylopoda, as an equivalent group (usually "sections") within the same suborder. This combination and some others which assign to the mouse-deer an even greater independent status is irrational. In spite of all their distinct characteristics, Tragulidae cannot be regarded as equivalent to Tylopoda and even less so to Suiformes. Additional characteristic features of Tragulidae are a very thin interocular septum and the fusion of the optic foramena into a single opening.

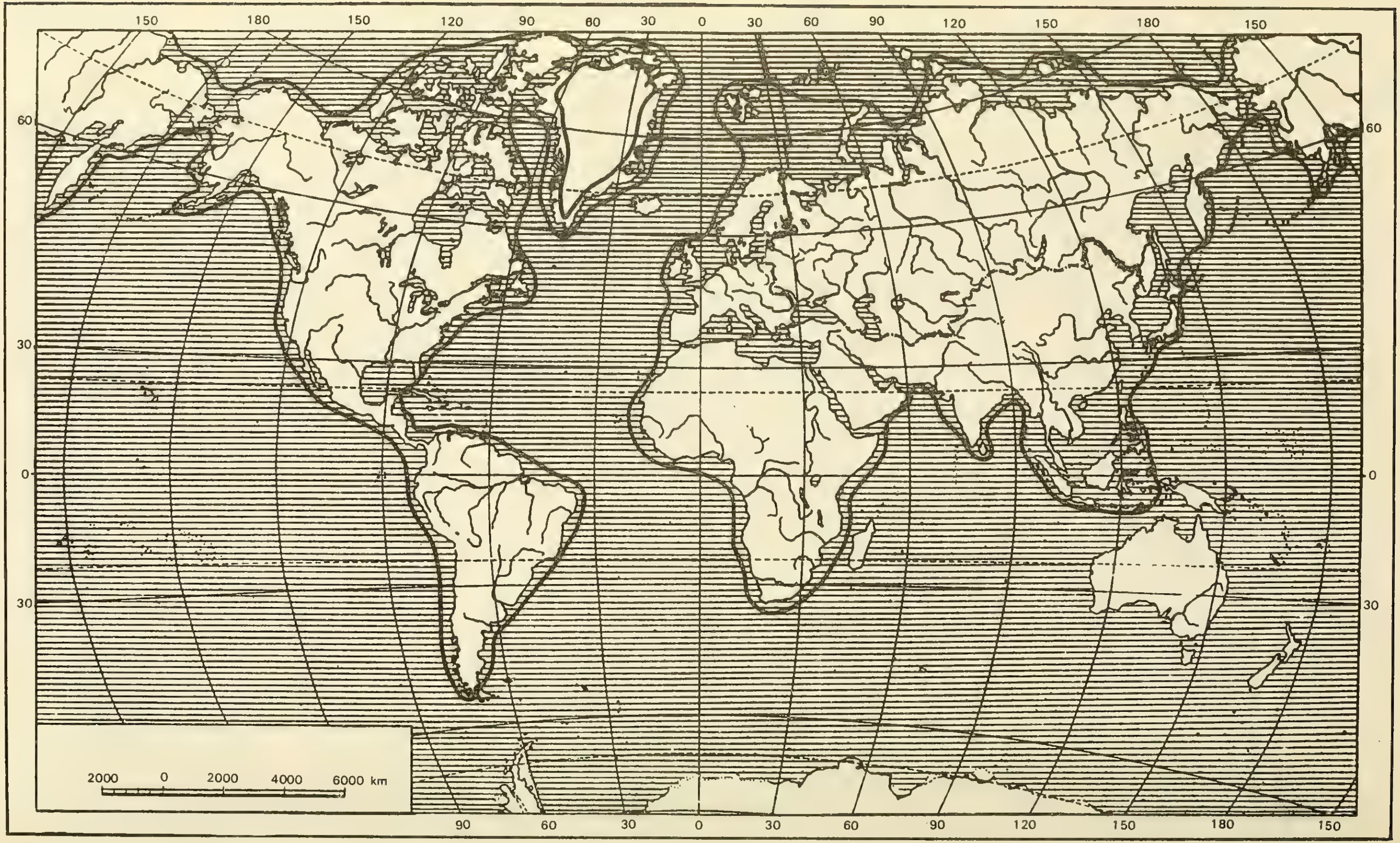

150
180
150
120
90
60
30
0
30
60
90
120
150
180
150
60
30
0
30
60
30
0
30
2000
0
2000
4000
6000 km
90
60
30
0
30
60
90
120
150
180
150

Fig. 24. Geographic range of suborder Ruminantia (reconstructed) (scale in km). V.G. Heptner.

(Europe, North America, and Asia). This group had evolved mostly in the Oligocene at the close of which its extinction commenced; however, an extremely small number of species have survived in the Recent epoch as relicts. Furthermore, Tragulina were evidently never particularly abundant. Pecora occur only in the Lower Oligocene (deer; Asia) and some groups even in the Lower or Middle Miocene (giraffe and Bovidae). Tragulina during the period of their greatest development evidently served as the parent group for Pecora. After the Miocene there was an exceptionally rapid development of Pecora, which became an extremely divergent, abundant, and flourishing group of artiodactyls (and ungulates in general), that survived until the end of the Tertiary period and flourish even now. This is particularly true of Bovidae. The remaining groups of Pecora developed relatively less evenly or recorded no special development whatsover; they have been reduced at present to groups which are becoming extinct (Antilocapridae and Giraffidae).

Until recently the taxonomy of supraspecific categories of ruminants (Pecora) was extremely imperfect[3]. At present, however, the basic features of the supraspecific categories can be regarded as fairly well understood and generally accepted. Some generic classifications of deer, more so the division of Bovidae into subfamilies (which until recently remained extremely artificial and arbitrary) constitute exceptions.

The taxonomy of various species of the suborder is relatively simple, but until recently had been studied little and not always along correct lines. The actual picture of the species composition of this group (especially of African forms) was understood only in the last decade. This led to a sharp (and as yet incomplete) reduction in number of species.

The suborder has been divided into two infraorders—Tragulina and Pecora. In toto the suborder comprises 255 genera (about 61% of all artiodactyls) placed under 15 families (60% of artiodactyls). Of these, 76 are extant (about 89% of extant artiodactyls), representing 5 families (about 55% of extant artiodactyls), and embracing about 132 species (about 88% of all extant artiodactyls).

Tragulina are classified into three superfamilies of which two are extinct and one extant—Traguloidea— comprising one extinct and one extant family—Tragulidae. The latter includes two genera (*Tragulus* and *Hyemoschus;* about 3% of genera in the suborder) with four species (three in southeast Asia and one in western Equatorial Africa; about 2.7% of species of the suborder).

---

[3] Partly due to vague ideas about species differentiation, Pecora until recently have been subjected to extremely diverse, often peculiar, taxonomic divisions. Almost every genus of deer has been raised to the rank of family by one taxonomist or the other.

75 Infraorder Pecora is divided into three superfamilies: Cervoidea (solid-horned or deer) with a single family (Cervidae), Giraffoidea (giraffe) with one extinct and one extant family (Giraffidae; Africa), and Bovoidea (hollow-horned) with two families—Antilocapridae (pronghorn; North America) and Bovidae (hollow-horned or oxen). Family Giraffidae includes one extinct and two extant subfamilies: Giraffinae (one genus, *Giraffa,* with two species) and Palaeotraginae (one monotypic genus, *Okapia*). Family Antilocapridae includes one extinct and one extant subfamily—Antilocaprinae with one monotypic genus (*Antilocapra*).[4]

Pecora comprise 74 Recent genera (over 97% of genera of the suborder) and about 128 species (97% of species of the suborder).

Many species are African in origin and fewer associated with Asia. In North and South America ruminants are few and poorly represented.

As the most abundant species of the suborder, ruminants are of utmost economic importance in all the features listed above (see characteristics of the order).

Fauna of the Soviet Union include one (Pecora) of the two infraorders, two (Cervoidea and Bovoidea) of the four superfamilies, and two (Cervidae or deer and Bovidae or hollow-horned animals) of the five families. The 18 species account for about 13% of species of the suborder or about 6% of mammalian species of the USSR. On the whole the group is not abundantly represented in the Soviet Union but is quite diverse.

Ruminantia are valuable game animals in the Soviet Union, providing important products for local consumption. (V.H.)

---

[4] Data on the composition of groups represented in Russian fauna are presented later under appropriate sections.

Infraorder PECORA Linnaeus, 1758

Superfamily CERVOIDEA Simpson, 1931

Family CERVIDAE Gray, 1821

76 Ruminants of moderate, small, or rarely relatively large size, with long legs; most are slender and light in build.

With some exceptions digits four. The lateral ones carry small hooves and usually have skeletal elements (phalanges); exceptionally they are relatively well developed and under certain conditions are of some importance in the movement of the animal. The metatarsal bones of digits II and V are completely reduced and only the upper or lower parts of the corresponding metacarpal bones are retained.

Facial part of lacrimals very well developed and, with few exceptions (*Moschus, Capreolus,* and *Pudu*), contain pits (depressions) for preorbital scent glands. Orbital region of lacrimals penetrated by two (exceptionally one) tear ducts. Ethmoid pit well developed and sometimes very large. Jugal greatly extended in facial part of skull; lateral surface of maxilla correspondingly shortened. Due to brachyodont dentition alveoli on maxilla shallow. Pneumatization of skull bones poor (lacrimal, maxilla, and anterior part of frontal). In forms with antlers, because of their growth, frontals usually greatly extended backward and parietals very much reduced. Orbit large and turned sideways. Premaxilla relatively insignificant in size. Tympanic bulla loosely articulate with skull, usually small, always tubular in shape, and generally with an uneven external surface.

In most species (exceptions, *Moschus* and *Hydropotes*) males, and in one case (*Rangifer*) females also, have antlers which are nonpneumatic projections (apophyses) of the frontals (not on separate bony formations called os cornu). Antlers consist of bony (not horny) material[1] (mesodermal) and are formed as processes (conti-
77 nuations) of apophyses of the frontals; they are shed once a year and grow again.[2] During the period of growth antlers are soft and

---

[1] Some researchers hold that the skin also participates in the formation of antlers and thus regard them, to some extent, as compound structures, not exclusively skeletal. In any case there can be no dispute about the basic differences in the formation and structure of antlers of deer and hollow-horns.

[2] The biannual shedding of antlers seen in *Elaphurus davidianus* is evidently the result of prolonged domestication.

covered with a hairy skin ("velvet"), which during antler ossification dies and sloughs. Antlers, with few exceptions (*Elaphodus, Mazama,* and *Pudu*), are branched, i.e., consist of a main beam with tines; fully developed among adults of various species, normally 2 (*Muntjacus*) to 20 tines occur.[3] At its base an antler exhibits a prominent ring ("rosette") with an uneven surface (channels through which blood vessels feed the antler during the period of growth).

Cheek teeth, at least the anterior ones, brachyodont. Roots, compared to size of crowns, small. Lateral vertical ridges on molars joined by horizontal ridge at base of crown, on boundary of its alveolar edge. Upper canine usually reduced; may, however, be absent altogether, or well developed, or even highly developed (particularly in males). Growth of canines related to development of antlers (particularly large in antlerless forms), quite prominent in species with poorly developed antlers, and rudimentary in forms with highly developed antlers. Dental formula:

$$\mathrm{i}\ \frac{0}{3},\ \mathrm{c}\ \frac{0-1}{1},\ \mathrm{pm}\ \frac{3}{3},\ \mathrm{m}\ \frac{3}{3}\ = 32 \text{ to } 34.$$

Integumentary glands well developed and diverse. Hair short and densely set. Color of adults uniform, dark, or sometimes with light-colored spots. In many species light-colored area ("speculum") present on rump. Sexual dimorphism prominent in majority of species; age-related changes also distinct. Spotted coloring of young animals (in large number of species) characteristic feature. Gall bladder, with few exceptions, absent. Placenta with few cotyledons.

Deer constitute a homogeneous family in which only a few species deviate markedly from the general pattern. These differences are not significant per se but associated with the absence or underdevelopment of antlers and a small body size (relatively large and complex antlers present in larger species). On the whole, the same set of characteristics are consistently seen throughout the family. The largest of the species (moose from Kenai, *Alces alces gigas*) attains a body length of 310 cm, height at withers 233 cm, and weight 770 to 815 kg (Anthony, 1928).[4] The smallest of the species have a body length of about 90 cm, height at withers about 51 cm, and weight 9 to 10 kg (*Hydropotes*) or even less (*Muntjacus reevesi* has a height of 40 to 45 cm at withers and *Pudu* 35 cm, i.e., the size of a large fox).

[3] Antlers of some races of *C. elaphus* with 32 or more tines represent a rare and extreme individual variation.

[4] These data, if not exaggerated, must refer to a very large specimen.

This group consists of mainly forest and partly forest-steppe species and a few tundra species. On the mountains they are found up to the upper limit of forests, entering into the lower regions of the alpine zone. Branches of trees and various species of shrubs form the major part of the diet of many species.

Deer have a relatively wide distribution. They inhabit the whole of South and Central America except for Tierra del Fuego and the West Indies, the whole of North America including the Arctic archipelago, the whole coastal belt of Greenland except the east coast, and Unimak Island (Aleutian Islands). In the Old World the geographic range covers northwestern Africa,[5] the whole European and Asian mainland up to and including Palestine, the Syrian part of United Arab Republic, and Mesopotamia in the south. In the north, the range covers Spitsbergen, Novaya Zemlya, southern
79 islands of Severnaya Zemlya, and the New Siberian Islands. In the south the range extends up to Ceylon and all of the island region between Asia and Australia in the east and southeast including Timor, Seram, Halmahera, and the Philippines.[6] The range also covers the east Asian islands, except the Kuril and Bering Sea Islands.

Extant forms of deer represent a very distinct, well-defined group of ruminants. In spite of sharp differences between extreme forms, there are no transitional forms between deer and other families. The peculiar structure of horns and their shedding in *Antilocapra* (pronghorn) are essentially unusual features of purely superficial similarity.

The family is, to a high degree, homogeneous. Numerous attempts to subdivide it into several families (see above) lack sufficient basis and have now been abandoned. Only musk deer (*Moschus*), which even now are sometimes regarded as a distinct family, stand apart prominently within the family.

[5] At present the geographic range of deer (*C. elaphus*) has shrunk very much. Formerly it extended into Algeria, Tunisia, and Morocco fairly extensively, but deer are now found only in a small section at the edge of Algeria and Tunisia (Heim de Balzac, 1936). Fallow deer (*C. dama*) were acclimatized in Egypt even in the distant past and are not a primitive species there. However, some data point to fallow deer being autochthonous in this region.

[6] Deer (*Rusa* complex) were acclimatized in New Guinea and New Caledonia. Even before the appearance of Europeans, the local inhabitants evidently raised deer on some islands. It is possible that some islands within the area under description were colonized thereby and the boundary described therefore may not be altogether natural. It is, however, difficult to establish it now. Probably, artificial colonization also influenced the development of some morphological characteristics throughout the island zone. This is true to an even greater extent of swine.

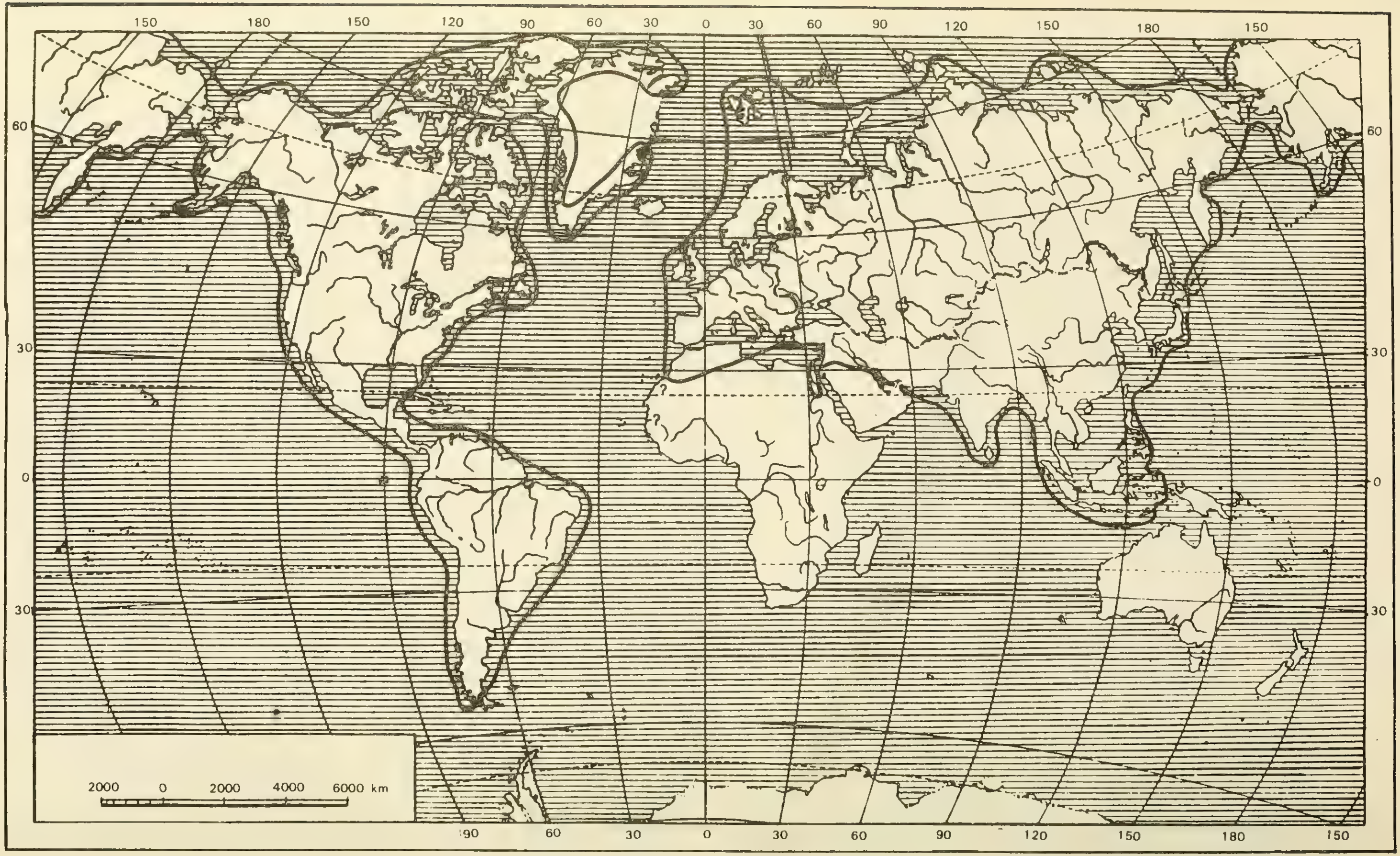

150
180
150
120
90
60
30
0
30
60
90
120
150
180
150
60
30
0
30
?
?
2000
0
2000
4000
6000 km

Fig. 25. Geographic range (reconstructed) of deer family Cervidae. Question marks refer to occurrence of deer *Cervus elaphus* L. in Rio de Oro and Senegal-Gambia (scale in km). V.G. Heptner.

Cervidae appeared in the Lower Oligocene (Asia) as relatively poorly differentiated forms, comprising the subfamily Palaeomerycinae, which became extinct in the Pliocene. This family is clearly linked with Oligocene Traguloidea and originated from them. Deer evolved from very small antlerless forms. One of the features of their evolution has been the acquisition and increase in size of antlers, which have become increasingly complex in the course of time. During their evolution no notable diversity developed in the deer family and they were not particularly abundant. They evolved relatively uniformly and at present, although not very abundant (fewer than Bovoidea), they represent a flourishing and extensively distributed group. The geographic range and population of deer, like those of all other large mammals, are at present diminished due only to man's intervention.

The family structure is simple. The time for further division into families and subfamilies and their separation into innumerable genera is well past, although the division of deer into various genera cannot yet be regarded as complete. Marked progress has been made in the separation of various species. The old method of intense subdivision and narrow interpretation of species is no longer acceptable, but partly still implemented for southeast Asia, particularly in the island region. This is largely explained by the development of complex structures in the animals of these regions.

The family is divided into seven subfamilies, two extinct (Palaeomerycinae and Dromomerycinae) and five extant: Moschinae (musk deer), Muntjacinae (barking deer), Hydropotinae ("water deer"), Cervinae (red deer or plesiometacarpal deer), and Odocoileinae (moose, Virginia deer, and related groups—telometacarpal
80 deer).[7] The family comprises 50 genera (about 19% of all ruminants),

---

[7] The classification presented here corresponds in its main features to that proposed by Simpson (1945), which is now widely adopted. One departure, recognition of the separate subfamily Hydropotinae, is supported by several researchers (Pocock, 1923; Allen, 1940; Ellerman and Morrison-Scott, 1951).

None of the prevailing schemes are very satisfactory since the subfamilies adopted are not of the same value in taxonomic importance. Strictly speaking, only two groups are distinctly identifiable within the family. One is Moschinae and the other includes all the remaining members of the family. On the other hand, there is no doubt that if subfamilies Muntjacinae, Cervinae s. str., and Odocoileinae are taken into consideration, linking *Hydropotes* to Odocoileinae is not in order, but the former should be isolated in the same manner as the other groups indicated above. Evidently, it would be more natural ultimately to subdivide the family into two subfamilies (Moschinae and Cervinae) and place the rest into a single suprageneric group, but of a much lower rank (tribe).

of which 17 are extant (Simpson, 1945)[8] (22 to 23% of present-day ruminants). The total number of species is 36,[9] i.e., about 24.3% of species of the suborder.

Cervidae are game animals providing meat, hide, often fur (mostly used by local inhabitants), and pharmaceutical material (European and Chinese medicine—antlers in velvet, tails, sex organs, and musk glands). Antlers are used for utilitarian and decorative articles; they are also valued as trophies. In the last century the population and range of most of these species were greatly reduced. One species (*Elaphurus davidianus*) has become extinct in its native land (China) with only several dozen animals preserved in zoos (England and Australia). Others face the threat of extinction and several survive under protection.

At some places deer are objects of intense hunting. Several species have been acclimatized outside their natural geographic range as game and ornamental animals (fallow deer in Europe and South America, sambar in Mauritius and Rodriquez, a few forms in New Zealand, reindeer in South America, and so on). One species (reindeer) exists in both wild and domesticated states. The degree of domestication is not very high. Experiments are underway for the domestication of moose. Some deer are held in a semidomesticated state in special farms for procuring their antlers in velvet (sika, maral, and Manchurian wapiti) or raised in zoos (fallow and Pere David deer).

The Russian fauna includes three of the five[10] subfamilies (Moschinae, Cervinae, and Odocoileinae), five[11] of the 13 genera (*Moschus, Cervus, Capreolus, Alces,* and *Rangifer*) (about 36% of extant genera), and six of the 36 species (about 16% of extant species). Deer constitute about 1.5% of species of Russian fauna.

In the Soviet Union members of the family are found throughout the territory except in steppe and desert zones. In the later zones they occur only in a few intrazonal points which are favorable for habitation.

---

[8] Eleven (Flerov, 1952) or 13 (Haltenorth and Trenze, 1957) is much closer to the actual number. Within the family the categories of subgenera are well substantiated. The list of genera given below should be referred to when discussing subfamilies.

[9] According to the data of Haltenorth and Trenze (1957). Lydekker (1915) recognized 48 and Flerov (1952) 50 species. These numbers are clearly exaggerated.

[10] Muntjacinae comprise two genera (*Muntjacus* and *Elaphodus*); a few species occur in south and southeast Asia. Hydropotinae (one monotypic genus) is found in eastern China and the Korean Peninsula.

[11] *Dama* is considered a subgenus. Moreover, fallow deer is not an indigenous species of the Soviet Union; it was acclimatized as a game animal.

The economic importance of deer in the Soviet Union has already been discussed. However, no intense raising of these species for use as game animals has been undertaken. Deer are also conserved in several preserves. Hunting of some species is totally or partially prohibited. (V.H.)

Key to Species of Deer (Cervidae)

1 (2). Antlers absent in males and females. Upper canines very large: in adult males project out of mouth; in females their length is greater than height of molars. Preorbital glands absent. Hind limbs almost 30% longer than forelimbs. Lacrimal without depression. Usually only one tear duct present. Body length of adult animals not more than 110 cm and maximum skull length 165 mm . . . . Musk deer, **Moschus moschiferus** L. (pg. 101)

2 (1). Antlers present in males and sometimes in females. Upper canines absent or poorly developed; their length not more than height of molars. Preorbital glands present and often well developed. Hind limbs only slightly longer than forelimbs. Lacrimal with depression, often large and deep. Tear ducts invariably two. Body length of adults exceeds 110 cm and maximum skull length more than 180 mm.

81 3 (6). Muzzle and area between nostrils entirely covered with hair or with only a very small bare patch on upper lip between nostrils (most of area between nostrils covered with hair).

4 (5). Space between nostrils entirely covered with hair; muzzle not enlarged. Vomer divides nasal passage so that pair of passages formed. Females with antlers . . . . Reindeer, **Rangifer tarandus** L. (pg. 430)

5 (4). Between nostrils small section of bare skin occurs but much of it covered with hair; muzzle of adults very much enlarged. Vomer does not divide nasal passage and hence latter not paired. Females without antlers . . . . Moose, **Alces alces** L. (pg. 307)

6 (3). Space between nostrils, sometimes neighborhood of nostrils, and entire muzzle bare.

7 (8). Tail very short, does not project out of fur, and not discernible externally. Preorbital gland poorly developed and pit half diameter of eye. Depression on lacrimal small and faint. . . . . .Roe deer, **Capreolus capreolus** L. (pg. 243)

8 (7). Tail well developed, projects out of fur, and invariably very distinct. Preorbital gland large (equal to or slightly less than diameter of eye). Depression on lacrimal large and deep.

9 (10). Tail relatively short; length (together with terminal hair) less than ear length. Tail not black at base. Speculum large and ocherous or with an ocherous tinge, but not pure white. Body size large; height of adult male at shoulders usually not less than 120 cm and maximum skull length exceeds 350 mm. Summer coat without spots or with stray spots along sides of backbone and top of back, usually in females. Antlers not flattened and with two tines in lower part of beam (brow and bez) . . . . Red deer, **Cervus elaphus** L. (pg. 159)

10 (9). Tail relatively long; length (together with terminal hair) more than ear length or almost equal to it. Tail with black, white fringed zone at base. Speculum white. Summer coat with bright, light-colored spots on back and sides. Only one tine (brow) at base of antlers.

11 (12). Body size, small; height of adults at shoulders up to 1 m or so. Tail markedly longer than ear. Hair around urinogenital orifice long and penicillate in arrangement. Upper canines absent. Antlers flattened at ends and shaped like a vertical shovel. Maximum skull length under 300 mm. . . . . Fallow deer, **Cervus dama** L. (pg. 981)

13 (12). Body size slightly larger; height at shoulders over 1 m. Tail nearly equal to ear length or slightly longer. Hair around urinogenital orifice not long and not penicillate in arrangement. Antlers not flattened at ends and not shaped like a shovel. Maximum skull length over 300 mm. . . . . Sika deer, **Cervus nippon** Temm. (V.H) (pg. 131)

Subfamily MOSCHINAE Zittel, 1893 (Musk Deer)

Size, small.

Toes four. Lateral ones relatively well developed with normal phalange skeleton; only distal portions of metacarpal and metatarsal bones of toes II and V present, while proximal portions reduced ("telometacarpal" ends). Lacrimal without depression for preorbital
82 gland. Orbital region of lacrimal pierced by single tear duct. Nasal process (pr. nasalis) of premaxilla reaches, or almost reaches, frontal, or only separated from it by ethmoid pit. Ethmoid pit small. Parietals normally developed (not reduced). Antlers and apophyses of frontals absent.

In males upper canine extremely well developed and projects out of closed mouth; it is sharp, points directly downward, and grows throughout life. Females invariably with canines but they are small. Dental formula:

$$i\,\frac{0}{3},\ c\,\frac{1}{1},\ pm\,\frac{3}{3},\ m\,\frac{3}{3} = 34.$$

Hind limbs markedly longer and more massive than forelimbs, giving animal an altogether characteristic appearance—posterior part of body notably more massive than anterior, very much raised, and locomotion saltatorial. Exposed anterior portion of muzzle large and surrounds nostrils. Tail very short. Preorbital and metapodial glands absent. Caudal glands and large musk gland on abdomen (in preputial region) present. Glands also present on outer surface of thighs (Yu.A. Salmin); glans penis with filiform protuberance. Gall bladder present. Teats two.

Molt occurs once a year.

Moschinae are montane forest (probably often alpine) forms associated with rocks and steep inclines.

Found in the Himalayas, China, including the northeastern part, the Far East, and eastern and central Siberia (see description of musk deer).

Musk deer, as mentioned in the family description, represents a distinctly different group of extant deer and their status as an independent subfamily is indisputable. Until recently some researchers have long been inclined, without much basis, to separate them com-

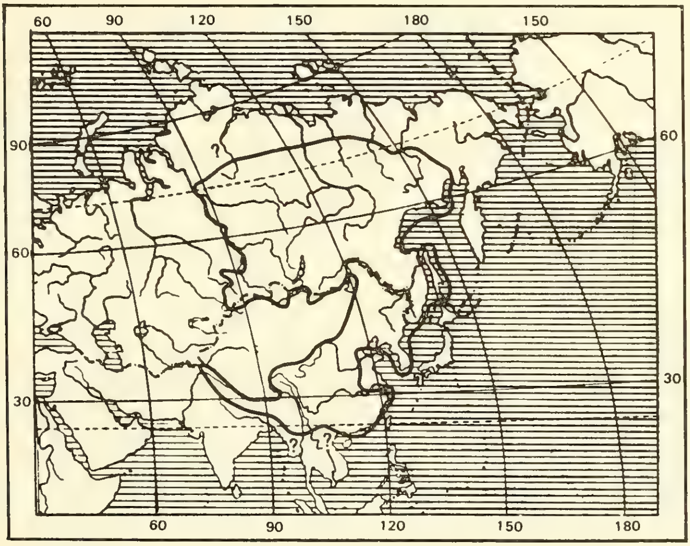


Fig. 26. Geographic range (reconstructed) of subfamily and genus of musk deer, Moschinae and *Moschus* L., and range of musk deer species *Moschus moschiferus* L. V.G. Heptner.

pletely from deer into a special family. Some even considered musk deer a connecting link between families Cervidae and Bovidae. This view, based on a few insignificant characteristics, has no adequate basis whatsoever, any more than attempts by some zoologists to place this group among Traguloidea.

83 Primitiveness of Moschinae among extant Cervidae is indubitable. Fossils of musk deer are known only from the Pliocene and probably Lower Pliocene of Asia, however, and even these belong to the Recent genus.

The subfamily is represented by only one genus (about 8 to 9% of extant genera of the family) with one species (about 3% of species of the family).[12]

Musk deer are caught for musk, which is used in the perfumery industry.

There is only one species in the subfamily, constituting about 0.3% of species of Russian fauna.

In the Soviet Union musk deer are distributed in central and eastern Siberia and in the southern part of the Far East. (V.H.)

Genus of Musk Deer

Genus *Moschus* Linnaeus, 1758

1758. *Moschus*. Linnaeus. *Syst. Naturae*. Ed. X, vol. I, p. 66. *Moschus moschiferus* Linnaeus (Opinion 75 of the International Committee on Nomenclature).

1848. *Odontodorcas*. Gistel. *Naturgesch. d. Tierreichs*, p. 82. *Moschus moschiferus* Linnaeus. See characteristics of the subfamily.

---

[12] Suggestions that the genus contains three species—Himalayan *M. chrysogaster* Hodgson, Szechwan *M. berezovskii* Flerov, and Siberian *M. moschiferus* Linn., or *M. moschiferus*, *M. berezovskii* Flerov, and *M. sibiricus* Pall.—according to another nomenclature (Flerov, 1930 and 1952)—have not been favorably received. Nevertheless, the extremely small Szechwan musk deer should be studied further from morphological and geographic points of view. To date only two typical individuals have been caught from the region where the much larger *M. m. sifanicus* Büch. lives. Prevailing opinion maintains that these two individuals are no more than extreme variants or even simply abnormally developed individuals ("starvelings") (Allen, 1940).

MUSK DEER

Moschus moschiferus Linnaeus, 1758

1758. *Moschus moschiferus*. Linnaeus *Syst. Naturae,* 10th ed., vol. 1, p. 66. Altai.[13]

1779. *Moschus sibiricus*. Pallas. *Spicil. zool.,* vol. 13, p. 29. Stanovoy mountains.[14]

1830. *Moschus altaicus*. Escholz. *Isis* (*Oken*), p. 106. Mongolia.

1911. *Moschus parvipes*. Hollister. *Proc. Biol. Soc. Washington,* vol. 24. Mountains at Mokpo in southern Cholla province, South Korea.

1928. *Moschus moschiferus arcticus*. Flerov. *Doklady Akad. Nauk SSSR,* p. 516. Mountains of Tulayakh-khaya, 460 km north of Verkhoyansk (northeastern branch of Tas-Khayakhtakh).

1928. *Moschus moschiferus sachalinensis*. Flerov. Ibid., p. 517. Aleksandrov, Sakhalin.

1954. *Moschus Moschiferus turovi*. Zalkin (Tsalkin). *Doklady Akad. Nauk SSSR,* vol. 46, no. 8, p. 366. Terney Bay in Sikhote-Alin sanctuary, Ussuri region. (V.H.)

Diagnosis

Moschus moschiferus is the only species of the genus.

84

Description

Musk deer in general appearance differ sharply from other deer and all other ungulates.

In build musk deer are slender and elegant. Their hind limbs are very long and well muscled; their forelimbs are relatively short, thin, and weak; and their chest usually small. Hence the hind quarters appear considerably larger, wider, and more massive than the anterior part of the body, the back highly arched, and the animal much higher at the sacrum than at the shoulders. With its small head and relatively thin, short, and fairly low neck, a musk deer looks "mournful" or "frightened". Even at a slow pace the animal moves with fairly long, extremely easy, soft, springy jumps, with its head lowered, emphasizing all the more its characteristic appearance. The above proportion of limbs and some other characteristics (elongation of head of femur, straightened pelvis, and others) designed for saltatorial movement are developed much more in musk deer than in any other ungulate, including even typical montane animals, and are undoubtedly advantageous for living in mountains and hills.

---

[13] Linnaeus distinguished "Tataria versus Chinam" forms. The nearest part of "Tataria" in the direction of "China" where musk deer are raised is Altai. This was accepted by several researchers and authors of monographs, including Soviet authors (Flerov, 1930; Tsalkin, 1947). There is no justification for altering this established view to regard "northern India" (Himalayas) as the type locality (Flerov, 1952). Furthermore, to do so would lead to needless difficulties in nomenclature (see Flerov, 1952).

[14] Stanovoy mountains are considered the type locality by Ellerman and Morrison-Scott (1951), probably based on the writings of Chaworth-Musters. Initially, Flerov designated "eastern Siberia" the type locality (1928 and 1930) but later opted for Altai (1952).

Head relatively small and elongated; eyes fairly large; ears long and broad, with fairly rounded tips, and extremely mobile. At tip of muzzle large bare patch of black coloration surrounds nostrils. Large, somewhat saberlike, fine, and extremely sharp canines project directly downward from mouth of male. Tips of canines in old males descend considerably below chin. Canines of females not visible externally. Tail very small and does not project out of fur. In adult males tail bare (only tuft of hair present at tip), flat, thick, with rounded end. In females and young males tail thin and covered with hair. Hooves of middle toes sharp, narrow, and drawn out. Lateral hooves relatively large, only slightly smaller than medial ones, sharp, and elongated; ends reach base of hooves of medial toes. Functionally, lateral hooves more active than similar structures in other Russian species of the family; in a standing animal they almost invariably reach the ground and are usually seen in hoofprints.

Fur consists of hair of several types. Much of body covered with long, somewhat wavy, coarse (up to 0.5 mm in diameter), and elastic hair which is highly pneumatic and hence quite brittle. Length of hair on sacrum reaches 95 mm and at withers 65 mm; on sides sometimes shorter, and even more so on neck and abdomen, especially on head and legs. Underfur relatively poorly developed, very soft, and delicate. Basal two-thirds of hair whitish and rest brownish-gray; tips dark brown or even blackish-brown. Some hairs with blurred, fairly broad, rust-colored band.

The overall coloration of the body of adult animals in full winter coat is dark chocolate or even dark brown, and fairly uniform throughout the body. Head gray with an admixture of brown on top. Ears grayish-brown on back side, dirty gray inside, and tips blackish. Upper side of neck dark chocolate with grayish tinge. Against this background usually a yellowish band occurs containing sometimes paired hazy spots. On lower side of neck a white or whitish band with an elongated medial brown patch extends from lower jaw. Light-colored band runs farther onto chest and inside surface of forelimbs. Color of sides somewhat lighter than that of back. Light brownish-ocherous or rusty-yellow spots scattered on sides and along back, which usually form longitudinal symmetrical rows. Two rows occur on the front and sides and five or six on the thighs. Two rows usually extend along back, sometimes almost merging into longitudinal bands. Abdomen and limbs brownish-chocolate and front and inner side of legs grayish.

Overall coloration of body exhibits fairly pronounced individual variations from light, almost yellow to brownish-black. Spots in
85 particular highly variable. Usually large, bright, and distinct, but sometimes small, dull, and blurred. Sometimes obsolete on sides but invariably preserved on thighs. Contrarily, sometimes number of spots so great as to give an overall ocherous-gray tinge to much of trunk. There are no sex-related color differences, or such differences are slight; spotting in females appears to be somewhat more intense. Seasonal differences manifested in fur color; it becomes lighter toward the end of winter as a result of wear and fading.

Molt occurs once and there is no summer coat as such. Commencing from the end of winter and nearly throughout the whole of the warm period of the year, old hair is lost and new commences to grow; this growth process ceases late in autumn. In summer the animal has short hair without underfur. Faded and worn remnants of old fur along with growing and already grown new hair are often seen on the back throughout summer (especially in nursing females).

Age-related changes in color and hair coat are prominent. In new-borns hair is short and relatively soft. Background color dark brown. Entire upper side of trunk (back, scapular region, upper part of the sides, forelimbs, and thighs) densely covered with spots, forming a distinct light-colored "saddle cloth". Spots yellowish-white or rust in color and often placed so that longitudinal rows (sometimes transverse also) form, which often merge into bands. On the croup and thighs, where the band is larger, as many as five rows may occur. Large whitish patch occurs on head and under ears; inner surface of ears light ocherous and outer part rusty. Upper side of neck with two large, light rust-colored spots. Throat white with yellowish hue. Two light-colored bands run along lower side of neck onto chest and on inner side of forelegs, where they reach lateral hooves. In addition to whitish field on throat, two small white bands on each side extend backward along posterior side of cheek and throat. Abdomen white with a yellowish tinge; groins and inner surface of hind legs white. By winter the young animal molts into its first winter coat, made up of coarse hair typical of adult animals, and resembling in color that of adults but with spots better developed. Second winter coat (at age 1.5 years) does not differ in color from that of adults.[15]

Caudal glands located on upper surface of tail contain a secretion which exudes a goaty smell. Musk glands enclosed in a special sac of skin located in front of preputial orifice. In adult males sac may reach about 3 cm in width and 4 to 5 cm in thickness. Both categories of glands are associated evidently with sexual activity (probably for marking territory); structure and function of other glands (on the thighs) not known. Mammary glands bare and two teats 14 to 15 mm long located close together.

Skull small with relatively well-developed cranial part and short facial part. Length of latter comprises 47 to 52% of maximum length of skull. Lacrimal flat and without depressions. Premaxillae with long nasal processes wedged between nasal and maxilla. Supraorbital processes insignificant. Parietal crests converge behind and form an indistinct arrow-shaped crest.

Teeth relatively small. Incisors and lower canines differ little in size and only slightly decrease in size from the center to the outside. Crowns flat and broad like leaves, fairly symmetrical (not bent to one side), and end ones somewhat superimposed on medial ones (canine on third incisor, third incisor on second, and second on first). Molars on lower jaw with well-developed additional tubercles on outer side. Upper canines of males highly developed and saber-like with very sharp tips. They are greatly compressed from the sides, the rear edge sharp and used for cutting, and the anterior surface more blunt. Length up to 70 or even 100 mm. Pulp cavity
86 exposed and grows throughout life of animal or for most of it. Tooth fits loosely in alveolus and when in use can move slightly forward, backward, or sideways. This evidently prevents breakage to some extent. Upper canines present in females but small, although not smaller than lower canines, and do not project out of mouth.

Sexual dimorphism in skull well manifested and associated primarily with varying degrees of development of canines. Entire frontal region of skull of males much more massive and broader than that of females. Sides of nasal region of male skull almost parallel, while in female converge forward like a wedge. Due to large size of alveolus of canine, premaxilla and maxilla in male large but nasal process of former lies almost horizontally. In females they are almost vertical. Palate in region of canines broader in males than in females. Supraorbital processes and zygomatic arch in females weaker than in males, and overall skull size of females somewhat smaller.

---

[15] Views regarding much longer series of age-related changes and maturity of animals only in the third year (Flerov, 1952) are erroneous (as explained later).

Age-related changes are more prominent in the skull of males than in females, due to progressive enlargement of canines with age. Consequently facial part becomes increasingly massive and enlarged in males, while in females it remains fairly uniform.

Vertebral column intensely arched. Posterior part large and relatively massive, while anterior part much slighter in build. Lumbar region massive and equal to thoracic in length. Chest short and narrow (Flerov, 1952). Length of hind limbs more than that of forelimbs (up to the shoulder joint).[16]

Size and weight of animals undergo relatively few changes. This is primarily true of age-related changes, since growth and maturity proceed rapidly and the animal is already fully developed by the age of two years. There are no perceptible sex-related differences in size and weight. Newborns weigh 300 to 500 g, adult females in Sikhote-Alin up to 15 to 17 kg, and adult males slightly less (Yu.A. Salmin). Overall body length 86 to 100 cm, height at winters 56 to 67 cm, rarely 80 cm, height at sacrum 67 to 80 cm, length of ears 8 to 11 cm, and tail length 4 to 6 cm. (V.H.)

Taxonomy

Moschus moschiferus is the only species of the genus.

Geographic Distribution

Inhabitants of eastern Asia, almost from the northern forest boundaries to southern China, Assam, and Burma. Also found in the Himalayas.

Geographic Range in the Soviet Union

Range in the Soviet Union very extensive and comprises about one-half of range of species, namely, almost the whole of its northern half. It covers the southern region of central Siberia, Trans-Yenisey, Siberia, and the Far East excluding the northeastern sector.

In the southwestern range musk deer occur in the Altai. Extreme southwestern habitats of musk deer in the Altai are Kurchum and Narym mountain ranges and the upper courses of the Bukhtarma (A.M. Nikol'skii, 1883; Kuznetsov, 1948; Antipin, 1941), i.e., probably the southern Altai mountain system.[17]

---

[16] More detailed information on morphological characteristics of species can be obtained from Flerov (1952) and Tsalkin (1947).

Musk deer are dispersed extensively throughout the Altai but it is impossible to establish precisely the boundaries of their range there, especially in the past. Encounters with musk deer are known in the Katunsk range, in the Koksa basin, i.e., Korgonsk (Abai and Koksinsk mountains), in the upper reaches of Charysh (Ust'-Kan), i.e., probably also in Tigerets range, and along the Cherga, i.e., in the
87 Cherginsk and Seminsk mountains. Farther east the range boundary runs to the northern extremity of Lake Telets (Kashchenko, 1899; Flerov, 1936; A.M. Nikol'skii, 1899; Yurgenson, 1938; V.G. Heptner). There is no positive information about the occurrence of musk deer in the western mountains of Ubinsk, Ul'binsk, and Ivanovsk Belkakh, but its habitation there, at least in the past, is highly probable. The boundary does not run up to the north of the range and evidently did not reach Gorno-Altai (Oirot-tury and Ulaly), because environmental conditions are unfavorable for the species.[18]

Farther away the range covers the Abakansk range, at least its southern part in the region of Lake Telets (V.G. Heptner) and the Kuznetsk Alatau (Flerov, 1935; Yanushevich and Blagoveshchenskii, 1952). Details of the distribution of musk deer in this zone are not known. In the Salair ridge it is evidently absent. East of the Altai, the range encompasses the Sayan mountains in the north right up to Krasnoyar (Stolba sanctuary) and the Tuvinsk district, and in the south includes Tannu-Ola.

The distribution of musk deer in the rest of the range (greater part of Siberia) is poorly known. It is described here in a very general manner. The boundaries of the range at several places have been outlined only roughly or even tentatively because of inadequate information. Yenisey serves as the western boundary of the range and musk deer do not go beyond it. Only in a few places such as Osinov rapids, near the mouth of the Podkamennaya Tunguska or in the region of Alinsk, near the mouth of the Elogui (S.P. Naumov,

---

[17] According to some data the range boundary is represented by the northern slope of the Narym range (Strautman, 1953). References to the Kurchum range pertain to its extreme northeastern section—from Altai village (now Katon-Karagai). Information about the propagation of musk deer in Saurakh (Kuznetsov, 1948) is not entirely accurate and calls for confirmation.

[18] References to the occurrence of musk deer in the environs of Biisk (Flerov, 1935) are undoubtedly erroneous and probably based on incorrect labeling of an animal in the collection.

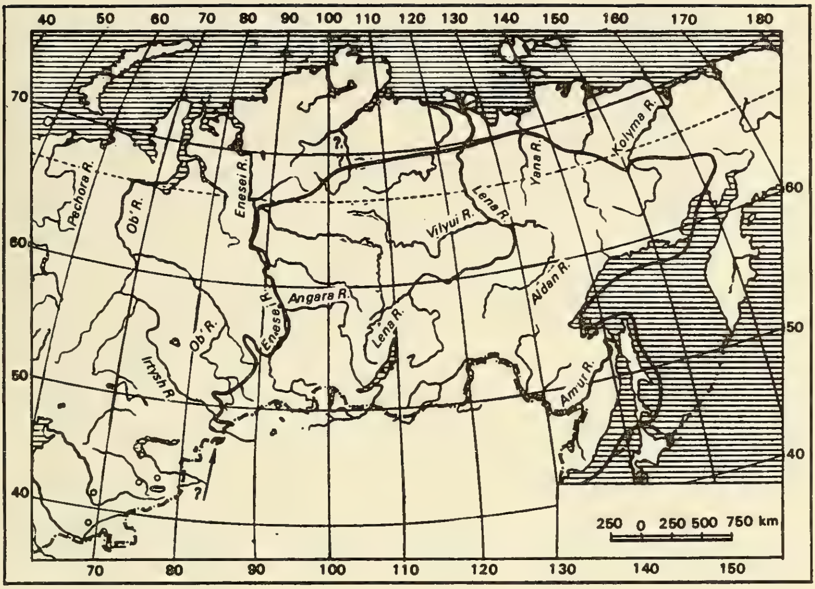

40
50
60
70
80
90
100
110
120
130
140
150
160
170
180
70
60
50
40
60
50
40
Pechora R.
Ob' R.
Enesei R.
?
?
Yana R.
Kolyma R.
Lena R.
Vilyui R.
Angara R.
Aldan R.
Enesei R.
Lena R.
Ob' R.
Irtysh R.
Amur R.
250 0 250 500 750 km
70
80
90
100
110
120
130
140
150

Fig. 27. Distribution boundaries of musk deer, *Moschus moschiferus* L. in the Soviet Union. Arrow in southwest part of range indicates occurrence in Saurakh; question marks in northern part pertain to finds in Khatanga (scale in km). V.G. Heptner.

1931), is it encountered on the left bank of the Yenisey, right on the river itself. The northern limit of distribution of musk deer along the Yenisey evidently lies at the mouth of the Lower Tunguska (N.P. Naumov, 1934). It probably penetrates slightly more to the north. East of the Yenisey, in the north, musk deer have been reported at Lake Nekongda (66° N lat.), on the Tembencha River (a tributary of the Kochechumo, the northern tributary of the Lower Tunguska), in the watershed of the northern tributaries of the Kochechumo, Embichima, and Yagtala (N.P. Naumov, 1934), in the Syverm mountains at 100° E long. (Middendorff, 1867). The possibility is not excluded of musk deer occurring even more northward in the Kureika basin and probably in the mountains of Putorana, where
88 living conditions for it are evidently favorable at places, but there is no positive information to support this assumption.[19] The species has been noticed on Lake Yesseiy (Tolstov, 1916) roughly at 69° N

---

[19] There is even a reference that "the latitudes of Turukhansk—middle reaches of the Tembencha River—represent the northern limit of transgression of some animals" (Podarevskii, 1936). This is roughly at 65° N lat.

lat. This evidently is the northernmost reliable point of encounter of the species in the Yenisey-Khatanga region.

According to some data, musk deer range along the Khatanga, up to 70° N lat. (Flerov, 1952), which, considering its distribution in the Yenisey region, is dubious and requires confirmation.

Throughout the immense range stretching from the Khatanga to the Sea of Okhotsk the distribution of musk deer and the northern boundary of its range are not known for certain and the few scattered references available cannot provide a correct picture. Thus, in the area between the Khatanga and the Lena musk deer are known from the sources of the Ikikit River (Ukykit), the left tributary of the Olen'ok (about 69° N lat.; Maak, 1859).[20] On the Omolon and in the lower reaches of the Yana musk deer have been recorded in the north up to 70° N lat., and for the Tulyakh mountains 460 km north of Verkhoyansk (Tugarinov, Smirnov and Ivanov, 1934).

The known distribution of musk deer in the Indigirka basin and Kolyma is very vague.[21] Judging from available information it can be assumed that musk deer have probably spread along the left bank of the Indigirka into the region of its watershed with the Yana and roughly up to 70°—up to the northern extremity of the Cherskii range. Along the right bank of the river, between it and the Kolyma, it hardly reaches north of 67°30′ N lat., which is the northern end of the Mom' range. Farther away the boundary probably encircles the Kolyma lowland from the south and runs into the Kolyma somewhere in the region of central Kolyma (Zyryanka) or slightly above it. In any case it encompasses the region of the right tributary of the Kolyma, i.e., the Korkodonsk (Tugarinov, Smirnov and Ivanov, 1934). Running farther through the upper reaches of the Omolon it intersects the Kolyma range at 64°, emerging on its eastern slope slightly short of the coast of the Penzhina Gulf; without crossing the Penzhina Gulf, it turns along the eastern slope of the Kolyma range south (Belopol'skii, 1932), forming the eastern boundary. Thus the northern part of the Kolyma range and the mountains along the right bank of the Lower Kolyma and the lower reaches of the Omolon, including the Anyui range, evidently do not fall within the range of musk deer.

---

[20] Maak (1859) emphasized the absence of musk deer along the Vilyuysk and pointed to its habitation only along the Chone, i.e., the right tributary of the Vilyuysk (around 62°). In his reference to Ukykit he himself doubted this and suggested that they could be assigned to mountain sheep. Probably musk deer were actually present, all the more so since in the section on sheep he does not cite these data. Transgressions of musk deer into Vilyuysk are known (Tugarinov, Smirnov and Ivanov, 1934). Data for Vilyuysk and Chone cannot, of course, describe the northern boundary of habitation of the species in this part of Siberia.

[21] The statement that musk deer probably reached up to 70° only in Indigirka and later descended to 69° (Flerov, 1952) is not supported by accurate data and appears incorrect. Even in the map shown in the same work the range runs much farther north. Precisely for the same reason the statement by Kolyushev (1936) about the habitation of musk deer in Yakutia up to the northern limit of the forest tundra is disputed.

The eastern boundary of the range of musk deer is formed by the mountains on the shore of Sea of Okhotsk reaching up to the sea coast (Abramov, 1954).[22] The boundary line due to local terrain conditions is fairly complex. Thus, for example, in the plains of the Amur estuary region musk deer are absent (Maak, 1859). Farther to the south, along Sikhote-Alin, the range evidently runs everywhere up to the sea coast or comes close to it.

The southern boundary of the range within the USSR is represented by the state boundary up to which the range reaches almost everywhere. Exceptions are the relatively small areas along Amur and Ussuri valleys and very insignificant sections in the steppes of southeastern Trans-Baikal, in the region of Kyakhta and the lower
89 reaches of the Dzhida. These areas, in spite of prevailing views, are extremely small and no more than "open spaces" in the range, also seen in the north.[23] In general, the range everywhere runs beyond the state boundary; only along Tannu-Ola (USSR) do the state and range boundaries merge in the south.

Musk deer are found in the northern as well as southern parts of Sakhalin, but are absent in the Shantarskiy Islands and Kamchatka.

Within the range described above, the distribution of musk deer is extremely uneven. This is explained by the animal's affinity for montane taiga and rocky sections and its pronounced stenotopic nature.[24] Therefore the detailed placement of the species as a whole in a given region is extremely complex; pockets of habitation of the animal alternate with areas of its absence. Regions of habitation can be considerable in area. The population of musk deer is also very uneven, which makes for a characteristic pattern of disposition of animals in individual pockets.

---

[22] According to some reports (Flerov, 1935 and 1952), based on old data, the boundary runs along the coast of Sea of Okhotsk but at some distance from it.

[23] Musk deer are therefore found even along the Nerchinsk range in the Borzya region and are also caught in Byrkov region, slightly east and northeast of Borzya. They have also been sighted along the Chikoya, especially in the Kransnochikiisk region, and are generally found "everywhere in southeastern Trans-Baikal regions" (Podarevskii, 1936).

[24] Evidently herein lies the reason for the absence of musk deer in the plains and lowlands of western Siberia, west of the Yenisey.

Geographic Range outside the Soviet Union

In Mongolia musk deer are found in the mountains of Kosogol (Hobsogol) region and from there southeast along the Selenga, part of the Khangai system to the south roughly up to 45 to 46°, and Hentei southwest of Ulan Bator, and the Bogdo-Ula mountains. Musk deer are evidently absent in the Mongolian Altai and along offshoots of the Great Khingan entering Mongolia in the east. In northeastern China musk deer have spread to all the mountain systems (Great and Little Khingan, Il'khuri-Alin, east Manchurian montane region, and Chanbaishan) and the range thus covers almost the entire country except the broad expanses at the center (Manchurian plains) and some other areas.

Farther, the range (reconstructed) covers the Korean Peninsula (details not known), eastern parts of Inner Mongolia (absent in the west) and northern China (Jehol, Hebei, and Suiyuan') except, of course, the desert of Ordos and Alashan, Shansi, and Shensi. The western part of the range covers the eastern part of the Nan Shan range in the west at least up to Lake Karanor (about 98° E long.), the Kukunor region (South Kukunor range and others), eastern edge of Tibet (Kama and the region of the tributaries of Huang Ho and Yangtze, Mekong and Salween), the southernmost tip of Tibet and the Himalayas, and in the west up to Kashmir and Gilgit. The southern boundary of the range in China and Indochina is not clear. Evidently it includes the northern montane parts of Assam and Burma and south China provinces, evidently including Yunnan. Available information about the penetration of the species under description into south Burma up to Pegu province (in the region west of the lower Salween) and in the eastern part of Indochina along the mountains up to Vietnam is rather dubious.[25]

The eastern boundary of the reconstructed range may be tentatively drawn along the sea coast or close to it along the eastern rim of hilly Nan'lin'. At present, since much of eastern China is densely populated, musk deer do not reach their natural eastern boundary. On the plains between the lower reaches of the Yangtze and Huang Ho and slightly north (toward Peking), i.e., in the Great China plains, musk deer have evidently been absent from time immemorial.[26] (V.H.)

---

[25] Data for southern Burma and Indochina are fairly old and unconfirmed. It is highly possible that confusion between musk deer and Tragulidae existed.

[26] The range of musk deer outside the Soviet Union is based on data from Bannikov, 1954; Flerov, 1930 and 1952; Tate, 1947; Ellerman and Morrison-Scott, 1951; and others.

Geographic Variation

The intraspecific taxonomy of the species, in spite of several studies completed to date, cannot be regarded as adequately understood.[27]
90 Various researchers acknowledge five to seven geographic races. Least understood are forms in the southern parts of the range (Himalayas, southern China, and Tibet). Within the Soviet Union two to four subspecies are distinguished (Tsalkin, 1947; Flerov, 1952). Worldwide nomenclature is far from consistent.

In the Soviet Union three subspecies can evidently be distinguished but the differences among them are extremely insignificant, the characters overlap, and more precise data are required before definitive separation is permissible.

1. Siberian musk deer, *M. m. moschiferus* Linn., 1758 (syn. *altaicus, sibiricus,* and *arcticus*). Relatively large with maximum skull length of 164 mm. Nasals constitute 41% of maximum skull length. Interorbital width in most specimens more than width across supraorbital processes. Nasals usually form a wedge-shaped figure at posterior end. Metacarpals and metatarsals long (former 128 to 148 mm and latter 172 to 189 mm). Color dark. Hair base white.

This form is found throughout the Siberian part of the range except the Amur and Sakhalin. Outside the Soviet Union it inhabits northern Mongolia. The range boundary in relation to the next form is quite vague.

2. Far East musk deer, *M. m. parvipes* Hol., 1911 (syn. *turovi*). Generally somewhat smaller than preceding subspecies. Maximum skull length up to 157 mm. Nasals relatively short and constitute about 38% of maximum skull length. Interorbital width invariably more than width across supraorbital processes. Nasals usually do not form wedge-shaped figure posteriorly; they are blunt instead. Metacarpals and metatarsals somewhat shorter. Color darker than that of preceding form, i.e., chocolate-brown. Hair base gray.

The range covers the Ussuri and Amur. Outside the Soviet Union this form is found in Korea and probably adjoining parts of northeastern China. This is a very poorly distinguished form and reflects a tendency toward reduction in overall body size from north to south. Sometimes Amur and Ussuri musk deer are placed under the Siberian form (Flerov, 1952).

3. Sakhalin musk deer, *M. m. sachalinensis* Flerov, 1929. Relatively small form. Maximum skull length 151 mm. In skull structure similar to Far East musk deer width of interorbital area less than

---

[27] See the characteristics of the subfamily given below for total number of species.

width across supraorbital processes, and very rarely almost equal to it. Metapodium as in preceding form.

The range covers Sakhalin Islands.

Information on the geographic variability of musk deer outside the Soviet Union is rather vague and often contradictory. The forms described call for a revision. The following forms should be singled out for special study: *M. m. berezovskii* Flerov, 1928 (Szechwan; very indistinct form, sometimes designated a special species); *M. m. sifanicus* Büchner, 1894 (central China, Kansu, and Szechwan); and *M. m. chrysogaster* Hodgson, 1839 (Himalayas—Kashmir, Nepal, and Sikkim; possibly identical with the preceding form). (V.H.)

Biology

Population. The distribution of musk deer is characterized by uneven dispersal. They are found only in some sections of the habitat and generally do not form large herds. At places where musk deer have long been protected the population density sometimes reaches 73 to 78 animals per 1,000 hectares of forest area (Boskonsk River basin in the Altai preserve, 1940 and Stolba preserve, 1952). At places where musk deer are caught in large numbers population density does not exceed 5 to 10 animals per 1,000 hectares (Shcherbakov, 1953; Shaposhnikov, 1956). Stolba preserve (46,500 hectares) contains in toto slightly more than 500 musk deer (Dul'keit and Kozlov, 1958).

Habitat. In the Soviet Union musk deer mostly inhabit the middle altitudes of montane taiga and are not usually found above 1,600 m. The animals, especially in winter, are attracted to relatively steep 91 slopes covered with coniferous forest (nut pine, fir, or spruce, and rarely larch or Scots pine). Favorite habitats are sections with rock outcrops which provide shelter from predators. A distinct preference is shown for northern shaded slopes where arboreal lichens abound and an ice crust does not form in winter. Musk deer are rarely sighted in smooth terrains or in places far away from rocks (in the Lena basin and upper courses of the Angara this phenomenon occurs more often than in other regions); hence their distribution is usually mosaic in pattern. In the northern parts of the range they inhabit elevations covered with coniferous forest or forest-tundra vegetation.

In summer musk deer spend at least part of the day in valleys of forest rivers, near mountain streams, and along sections with good grassy vegetation where coniferous taiga alternates with mixed deciduous forests. They avoid marshy forests.

Male musk deer, especially in winter, live at a slightly higher

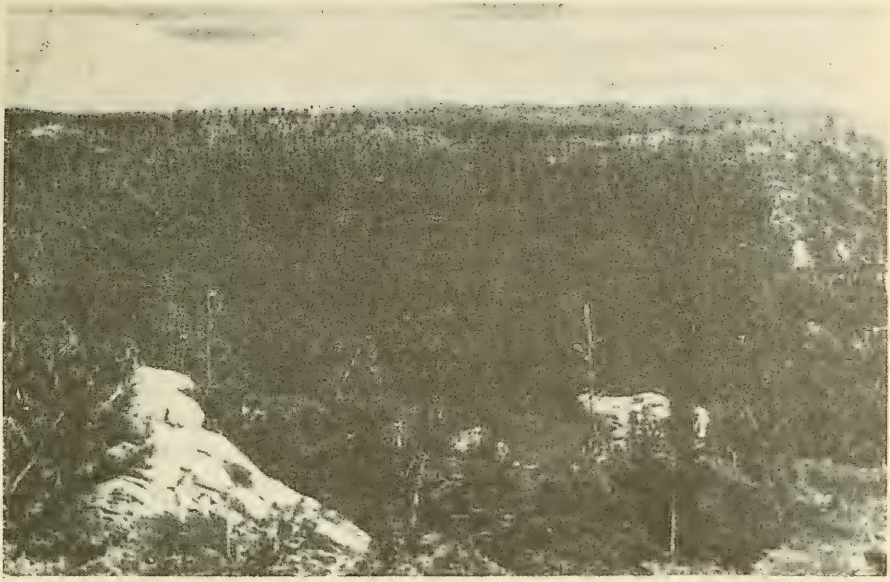


Fig. 28. Habitat of musk deer in eastern Sayan. Region of Lake Medveshi. July, 1956. Photograph by K.T. Yurlov.

elevation than females; they are absent altogether on gentle slopes (Sayans and Altai).

South of the Soviet Union's boundary musk deer inhabit mountains covered with deciduous forest and shrubs in sections where arboreal lichens are totally absent. *Moschus m. berezovskii,* which is close to the Siberian musk deer (Szechwan and Kansu), is confined to the alpine belt, however (Flerov, 1952).

Food. Over 130 plant species are known to be consumed by musk deer (Shcherbakov, 1953). Of these, about 20 constitute the main diet. In the Altai musk deer consume not less than 95 plant species, of which 9 are particularly important (Shaposhnikov, 1956). In the diet of musk deer lichens, primarily arboreal lichens (several species of *Usnea, Parmelia,* and *Evernia*) and to a lesser extent terrestrial bushy lichens (*Cladonia* and *Cetraria*), play an important role year-round. Lichens are of particular importance in winter, when they constitute up to 70% by weight of the stomach contents of musk deer. In Stolba preserve the stomach contents of 31 musk deer caught in winter contained almost invariably considerable quantities of lichens; in summer lichens were found in 50% of the stomach contents examined and in very small quantities (Shcherbakov, 1953). In the Altai lichens predominate in the food of musk deer from Sep-

92 tember through May (Shaposhnikov, 1956). In captivity musk deer consume about 0.8 kg lichens per day (A.G. Kostin).

Musk deer avidly consume arboreal food year-round. This includes thin branches and young shoots, coniferous needles and bark (mainly in winter), leaves, buds, and rarely small rootlets. Arboreal food in winter is second in importance to lichens. Musk deer consume mountain ash, aspen, maple, willow, bird cherry, honeysuckle, and other deciduous species; in winter they often nibble needles and end branches of fir, sharp-edged yew (in Sikhote-Alin), and rarely Scots pine and nut pine (Doppel'mair, 1926; Scherbakov, 1953; Shaposhnikov, 1956; Yu.A. Salmin). Needles evidently constitute a compulsory food. In Stolba preserve in winter needles have been found in almost all the stomach contents of musk deer and usually in considerable quantities. However, in captivity, when more satisfying food is available, the animals do not touch needles (Shcherbakov, 1953). Musk deer avidly consume in summer leaves of common sweetbriar (Stolba preserve) and in winter terminal branches and leaves of rhododendron (Sikhote-Alin). In the Irkutsk region musk deer consume nuts of Siberian pine (Kopylov, 1950).

Herbaceous plants serve as the main summer food of musk deer. At this time of the year they avidly consume buckwheat, umbelliferous plants, burnet, spirea, geranium, Gmelin peavine, leaves of bilberry and stone bramble, some grasses, etc.; the total weight of green mass in a stomach can weigh up to 2 kg (Shcherbakov, 1953; and others). In winter the dry parts of the following plants are also consumed fairly regularly but usually in small quantities: aconite, cow parsnip, willow herb, ferns, grasses, sedges, roots of some plants, and remnant green stalks of bilberry and horsetail (Kopylov, 1950; Shaposhnikov, 1956; and others).

In the Altai musk deer consume green moss (*Mnium cuspidatum*), the roots of arboreal ferns, and pileate mushrooms (birch mushroom, pepper mushroom, and others). Sometimes, musk deer successfully feed on mushrooms stored by squirrels among twigs (Shcherbakov, 1953; Shaposhnikov, 1956). In summer the food of musk deer is much diverse than in winter.

Musk deer obtain conifer needles and arboreal lichens not only from trees (up to a height of about 1.5 m) by standing on their hind legs, but also from windblown dry branches and sometimes forest clearances. Musk deer dig up food from under the snow only when the cover is no more than 20 to 30 cm deep (A.G. Kostin and F.D. Shaposhnikov).

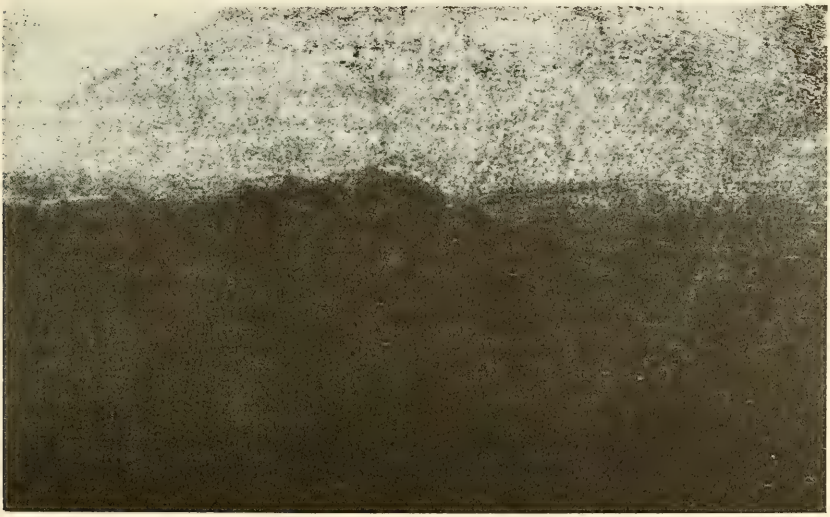
In summer musk deer periodically forage in those state farms least visited by other ungulates. In captivity they take salt but only a small quantity.

Home range. Musk deer live for most of the year in a home range of 200 to 300 hectares, holding onto it steadfastly. Such a home range comprises steep rocky "shelters" and more gentle slopes for feeding. The size of the home range decreases perceptibly in the second half of winter. In summer and during estrus musk deer wander extensively (Shcherbakov, 1953; Shaposhnikov, 1956; and others).

In a fir forest in Stolba preserve the average distance of daily movement of musk deer in winter was 3.8 km and in a pine grove with less abundant lichens, 4.3 km (Shcherbakov, 1953). In the Altai the distance covered daily on snow was roughly 4 to 5 km. On being chased musk deer usually run round and round in circles within their home range (F.D. Shaposhnikov).

Musk deer usually live singly or in groups of not more than two or three animals (adult female with young) and the habitats of this species are more isolated than those of other hooved animals. However, many musk deer go to distant places to feed on lichens, which are more readily accessible; some travel as much as 5 to 7 km (Shcherbakov, 1953).

Daily activity and behavior. Musk deer are active at twilight or at night. In summer the animals descend from their lair soon after sunset and feed in forest meadows and river valleys and near small brooks, reascending 100 to 200 m to their lair by morning. The lairs



93 **Fig. 29. Habitat of musk deer in the Altai sanctuary. Gorge of the Chira River visible in foreground. August, 1951. Photograph by F.D. Shaposhnikov.**

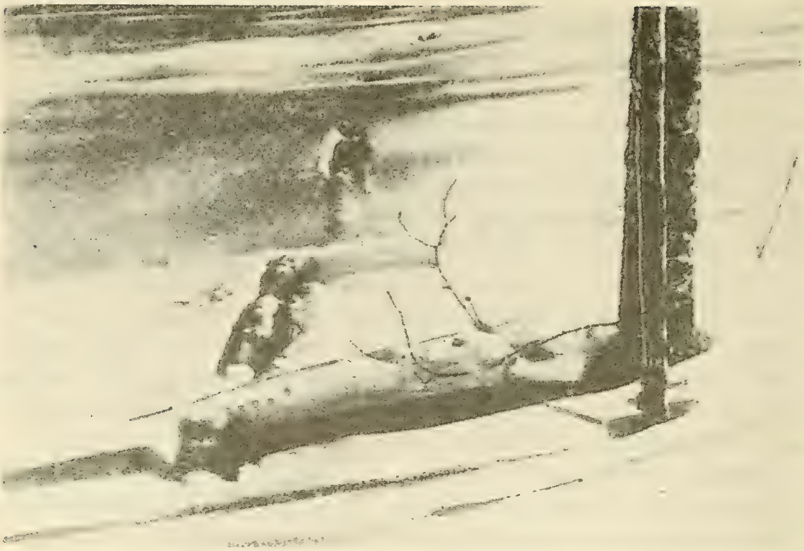


Fig. 30. Track of musk deer in deep snow. Upper course of the Kansk River. Eastern Sayan. March, 1952. Photograph by K.T. Yurlov.

93 are set close to rocks and sometimes among rock debris and along crests of narrow mountain ranges where, because of sparse forest, the wind is strong and hence mosquitoes and midges few. Musk deer lie comfortably at the edge of precipices, on the trunks of fallen trees, rocks, and so on (F.D. Shaposhnikov; and others). In the mountains of Sikhote-Alin musk deer are often troubled by blood-sucking flies when in dense grass, or moving near stumps or among brushwood left behind after floods. In such circumstances they remain during the day in river valleys (Yu.A. Salmin). Inside the lair the animals remain hidden and permit close approach. The lair is located in a fixed place.

94 In winter musk deer are active only for part of the night and usually lie down one to three times during the hours of darkness. In heavy snowfall and inclement weather the animals are less active (F.D. Shaposhnikov) and lie down at places which provide protection from the wind.

"Musk deer have long mobile toes ending in sharp and hard hooves which are extremely tenacious and provide the animal grip not only on the slopes of steep hills, but also on trunks of fallen or steeply inclined trees" (Yu.A. Salmin). Their gait resembles that of a rabbit. Musk deer invariably use the same pathways and thus form permanent tracks. In winter this beaten track facilitates movement on loose snow.

Information about the sense organs of these animals is contradictory. It is generally acknowledged that vision is keen, hearing good, and sense of smell poor.

Seasonal migrations and transgressions. Musk deer lead a fairly well-settled mode of life in most of the range in the Soviet Union. Where seasonal migrations do occur, they seldom exceed 1.0 to 5.0 km. Depending on topographic features, the animals live in winter at roughly the same altitudes as in summer, or in some regions 200 to 300 m (vertical height) below the summer altitudes or, contrarily, above them. In winter in mountains of central Sikhote-Alin musk deer live in high elevations and along mountain slopes (Yu.A. Salmin). Changeover to winter habitats occurs imperceptibly but usually takes place during September.

In winter musk deer prefer dense boreal forests. The weight distribution on the hoof (80 to 120 g per cm^2 of resting surface; Dul'keit, 1956) is relatively low and the minimum for ungulates. Their dependence in winter on food available above the snow such as arboreal lichens and branches of trees and shrubs enables musk deer to live even in extremely snowy regions in winter, but they are confined to extremely steep slopes. In less snowy sections (with a snow cover of not over 50 cm), deer move not only along mountain peaks but also along relatively gentle slopes (Dul'keit, 1956). In spring, with the appearance of thawed patches, many animals can be seen on southern slopes, moving away from them with the approach of summer.

Reproduction. In the Altai, Sayans, Yakutsk Autonomous Soviet Socialist Republic, Chita region, and Sikhote-Alin, musk deer usually come into estrus in December (in the Altai and Yakutia from the end of November) and the period generally extends over three to four weeks. However, according to Yu.A Salmin estrus in musk deer in central Sikhote-Alin occurs from early November to early December, i.e., almost a month earlier than in the Altai. In Stolba preserve estrus in musk deer continues throughout the whole of November and most of December. Among males spermatogenesis commences before rut in September and extends through February. In females no distinct pre-estrus stage is evident as the follicles are formed throughout the year (Shcherbakov, 1953).

Unlike other periods of the year in which herd formation is not at all characteristic of musk deer, during the period of estrus groups of three or four adult animals and in very rare cases even up to five to seven (two males and three females, three males and four females, etc.) can be seen. The young live independently. A male may mate with several females. A single female sought by several males is also

not rare. A more powerful male attempts to chase away the weaker but does not generally use his canines for this purpose.[28] Males emit a low squeal or "hiss" (Belousov, 1928; Shcherbakov, 1953; Shaposhnikov, 1956). The site of musk deer in estrus is recognizable by characteristic "stamping" of the ground and crushed grass. An excessive exudation of musk in males in rut evidently exerts a stimulating influence on females in heat. At the end of the rutting period, in early January in the Altai, musk deer groups break up (Shaposhnikov, 1956). The gestation period of musk deer is 185 to 195 days and there is no latent stage of embryonic development (Shcherbakov, 1953; Shaposhnikov, 1956). The female usually delivers two, rarely one, or even more rarely three fawns. However, in Stolba
95 preserve, of 13 pregnant musk deer examined, 9 had a single embryo and 4 had two each.

Most females fawn in June and some in May or early July. In the Altai isolated births of fawns have been recorded right up to July 12 (A.G. Kostin). In Sikhote-Alin fawning even commences at the end of April (Yu.A. Salmin) and the last fawns are born one month earlier than in the Altai. Fawning usually occurs in secluded places such as dense shrubs, under low branches of fir, in the proximity of fallen trees, etc. In Sikhote-Alin up to one-third of adult females remain barren every year (Yu.A. Salmin).

Musk deer attain sexual maturity at the age of 15 to 17 months (Shcherbakov, 1953).[29]

Growth, development, and molt. Fawns remain helpless for quite some time and the mother does not lead them out until the end of July or early August. She conceals herself and, in the event of danger, tries to drive away the enemy (Shaposhnikov, 1956). Suckling lasts up to the end of August or early September and the fat content of the milk may reach 19%. Fawns lead an independent life from autumn or sometimes from spring of the following year (Shcherbakov, 1953; Shaposhnikov, 1956; and others).

Newborns weigh from 300 to 500 g, rarely more. In Stolba preserve three-month-olds weigh 4.0 to 4.5 kg, which increases to 6.0 to 7.0 kg by the fifth month. In the Altai in winter young deer weigh 7.0 to 9.0 kg (Shcherbakov, 1953; Shaposhnikov, 1956; A.G. Kostin; Yu. A. Salmin). Adult males and females are almost equal in weight. In

---

[28] In discussing rut in musk deer in eastern Siberia, the Far East, and Mongolia, Cherkasov (1884), Abramov (1954), and other researchers mention vicious fights among males during this period which probably is an exaggeration.

[29] Flerov (1952) erroneously placed the onset of sexual maturity in musk deer in the autumn of their third year.

Stolba preserve the weight of males averages 13.3 kg (maximum 16.5 kg) and of females 13.7 kg (maximum 16 kg). Three adult musk deer caught in winter in the Altai weighed 10.3 to 16.8 kg. In Sikhote-Alin adult females weigh 15 to 17 kg (Shcherbakov, 1953; Shaposhnikov, 1956; A.G. Kostin, Yu.A. Salmin).

Juvenile hair molts three to five months after birth and subsequently the young differ very little from adults in color. At about one-and-a-half years of age coloration is identical to that of adults (Shcherbakov, 1953; Shaposhnikov, 1956).

Secretion of the musk gland commences in males at the age of four to five months (Shcherbakov, 1953) and milk teeth are shed in the second year. By the end of that year milk canines have been replaced with permanent canines in males; in three-year-old males their length often exceeds 60 mm and they become increasingly curved.

Molt in musk deer is a remarkably slow process, continuing from mid-February or early March to October or early November. Molt is most intense in April and May when the underfur is shed and the pelage of the animals extremely sparse. Molt commences from the limbs and head, then the abdomen and sides, and last to the croup. New hair grows slowly and the back is covered for almost the entire summer with a "saddle" of old, highly faded hair, dirty yellow in color (Yu.A. Salmin; and others). Among pregnant females the commencement of molt is somewhat delayed (Shcherbakov, 1953). There is no autumn molt among musk deer.

The life span of musk deer has not been definitively established.

Enemies, diseases, parasites, mortality, competitors, and population dynamics. Predators from whom musk deer suffer most are lynx and wolverine and in the mountains of Sikhote-Alin, yellow-throated marten; wolf and the rare tiger cause much less damage. In Stolba preserve musk deer remains have been found in 43% of the feces of lynx (117 specimens) gathered over a period of three years, mainly in winter (Shcherbakov, 1953). In Altai preserve musk deer remains were found in four of eight fecal samples of lynx collected in July to November. Musk deer badly mauled by wolverines have been found time and again in Altai preserve and once the chase of a single musk deer by two wolverines was observed (Shaposhnikov, 1956).

In the central parts of Sikhote-Alin the yellow-throated marten is the main enemy of musk deer, especially in autumn and winter when these predators hunt in family groups. The damage caused by marten greatly increases in the event of ice crusts, which greatly facilitate chase of the quarry. In the winter of 1935 to 1936, on the ice

96 of the Arma River basin, over a distance of 200 km the remains of 26 bodies of musk deer torn to pieces by martens were found (Yu.A. Salmin). In spring and summer young deer are particular victims of martens. The population dynamics of marten in some years depends greatly on the population of musk deer (Bromlei, 1953 and 1956).

Only in rare cases do musk deer become the quarry of brown bear. In the Altai, of the 180 samples of feces of this predator examined, the pelage of young musk deer was found in two (Shaposhnikov, 1956). Kaplanov (1948) found the remains of musk deer torn to bits by a litter of tigers in Sikhote-Alin mountains. In very rare cases sable, red fox, horned owl, and golden eagle attack musk deer (Kozhanchikov and Kozanchikov, 1924; S. Naumov, 1931; Shaposhnikov, 1956). Remains of musk deer killed by martens are often consumed by Siberian weasels (Bromlei, 1953).

In rescuing itself from a pursuer a musk deer will attempt to climb onto a rock, into a "shelter," or finding neither run in circles. A marten tries to cut across the deer's arc or chase it onto ice. Musk deer can run exceptionally fast only for 200 to 300 m and thereafter tire. Dogs and wolves soon outstrip musk deer over relatively level surfaces (Cherkasov, 1884; Bromlei, 1953 and 1956). Evidently predators constitute one of the reasons for the absence of musk deer on relatively gentle slopes, away from rocks.

The diseases musk deer suffer from have not been studied much. In autumn of 1919 in the mountains near Lake Telets dozens of bodies of musk deer were found, which had died from some unknown disease. According to old hunters such an epizootic has occurred only once (A.G. Kostin). In zoological parks mortality of musk deer due to necrobacillosis has been recorded. A musk deer which survived in a zoological park for three years (a record!) died of tuberculosis (Kadenatsii, 1958). In the Soviet Union, under conditions of zoological parks, 11 species of helminths have been identi-

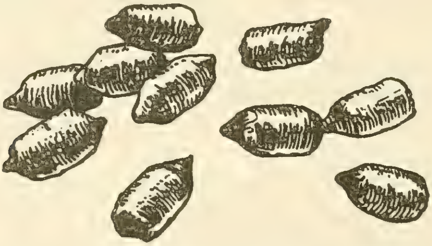


Fig. 31. Winter feces of musk deer (magnified). Primor'e territory (from Formozov, 1952).

fied for musk deer—2 species of cestodes and 9 species of nematodes. However, some of these are parasites transmitted by other animals. Under natural conditions musk deer serve as hosts most often for *Setaria cabargi* and *Pneumocaulus kadenazii* (Kadenatsii, 1958). Parasites found in musk deer in the Altai include *Cysticercus taenuicollis* and *Dyctyocaulon* among others (Shaposhnikov, 1956), in Kazakhstan—*Nematodirus* (Sokolova and Boev, 1950), and in Sikhote-Alin—*S. cabargi, Taenia hydatigina,* and *Monieza expansa* (Kadenatsii, 1958).

Musk deer are greatly troubled by mosquitoes, midges, ticks, and other insects. More than a hundred ticks were removed from the body of a musk deer on one occasion (Stolba preserve; Shcherbakov, 1953). Almost 2,000 larvae of *Pavlovskiomyia inexpectata,* a parasite of the dipteran group, were found under the skin of a Ussurian musk deer. Such musk deer become greatly emaciated and in summer their back, neck, shoulders, and croup are completely ulcerated (Abramov, 1954).

Musk deer have almost no competitors. In winter in the Altai musk deer quite often consume lichens fallen from the branches of trees shaken by the antlers of maral or broken by bear (Shaposhnikov, 1956).

Information on the population of musk deer is inadequate. In many regions of the Soviet Union, particularly in Primor'e, musk deer increased markedly immediately after their hunting was restricted in the 1930's and destructive methods of catching them prohibited. Among captured musk deer the sex ratio varies from 4:6 to 6:4 in favor of males.

Field characteristics. Musk deer are the smallest deer inhabiting the USSR and have a characteristic color that makes it impossible to mistake them for other ungulates. Seasonal differences in their fur color are insignificant. Neither males nor females bear antlers. In the field the color of their coat makes sighting difficult. The canines
97 project beyond the upper lip in males three or four years old or more but never in females. The usual sound emitted is a faint hiss. The hind legs are much longer than the forelegs and during rapid jumps extend beyond them, due to which the hoofprints resemble those of hares. On level ground the deer can jump a distance of up to 4.0 m; more often, however, this distance is not more than 2.5 m. A frightened animal may jump up to 4.7 to 5.0 m. On snow, walking prints measure 25 to 30 cm between steps (Dul'keit, 1956).

The toes are capable of considerable movement and hence hoofprint dimensions vary widely, depending on terrain and pace. In general they are smaller than those of other taiga ungulates but similar to those of mountain antelopes* (Formozov, 1952). In winter it is very easy to identify hoofprints as male or female from the form and position of the "urine spot" on the snow. In addition to tracks, hoofprints, and lairs, the presence of musk deer is also revealed by a unique feature—multiple feces deposited in one place. Fecal pellets are very small (0.7 to 0.8 cm × 0.35 to 0.40 cm) (Formozov, 1952); those of males have a pungent "goaty" smell (Shaposhnikov, 1956). (A.N.)

Economic Importance

Musk deer are caught mainly for musk ("musk deer perfume"), present only in males. Musk is secreted by a saccate gland located between the sex organs and the naval. In the middle of the last century several thousands of musk sacs of musk deer were exported from Russia to China through Kyakhta every year (maximum in 1855—81,200 sacs), but later the animal stocks evidently diminished greatly. In the hunting season of 1927 to 1928 in the USSR 5,089 musk sacs were collected by a centralized organization (Yakutia—114, Far East—3,136, and Buryat-Mongol Autonomous Soviet Socialist Republic and eastern Siberia—1,839). Another 193 sacs were collected in the present Tuva autonomous region (Nasimovich and Rudanovskii, 1935). Today several thousand musk sacs are collected annually. Musk deer stocks are evidently not fully utilized at some places, while in other regions the population of this species is low.

In the past musk was used in medicine in Europe and the East and musk imported for this purpose from Siberia for a long time. Musk as a natural perfume base in preparing high quality scents was discovered later.[30] Musk owes its sharp smell to muskone, a ketone-type compound present to the extent of 1 to 2%. Musk is also used in the preparation of scented artificial baits in catching predatory animals. The weight of a musk sac with contents in an adult deer ranges from 20 to 52 g; the actual musk weights 15 to 30 g, on the average about 20 g. In immature animals the musk content is much less. In the period of rut part of the musk is used by the animal and its reserves restored within two or three months (Shcherbakov, 1953).

The hide of musk deer is not durable as it has brittle hairs which deteriorate rapidly. Local people make leggings, mittens, and sleeping bags out of deer skins as well as use them for rugs. A thin but strong chamois is made from shaven skins and used for pillow cases, gloves, etc. The hair is used as mattress stuffing (Abramov, 1954).

---

*Reference not clear; possibly goral—Sci. Ed.

[30] A satisfactory substitute for musk is the synthetic preparation "tibetolite".

The meat of musk deer is lean and poor in quality; it is most often used as bait for catching sable and other fur-bearing animals or dried and stored for dog food. The canines are converted into various articles.

In the past musk deer were caught mainly in the countryside (enclosed and open pastures) by setting nooses or digging pits in their tracks. Nooses set up in tracks were the most common method. The end of the noose was tied to a stick which the musk deer could drag for some time, until it caught fast in something, after which
98 the loop tightened on the animal (Petri, 1930). A large number of animals were caught by trapping (with nooses and sticks) and placing other mechanical catching devices on their tracks. In summer hunting used to be done by shooting; the hunter used a birch pipe to imitate the call of a female deer and thus attract adult males and females. These methods of catching musk deer are now banned. The animals are shot from a concealed position, or caught by chasing, or bagged by some other method. Sometimes dogs are used to chase musk deer toward the hunter or for keeping the animal at bay. Deer are shot with bullets and buckshot. Hunting usually occurs from September 1 through March 1 (in some parts for a much shorter period) and generally requires a license. In 1954 hunting for musk deer was prohibited in northern Kazakhstan, the Altai, Krasnoyar region, and Sakhalin.

Some methods of catching musk deer live are also known: nets (successfully used in the Altai), nooses set at the end of a pole (to catch the animal emerging from its "shelter"), and other methods makes a preferential catch of adult males possible.

From the end of the 1930's to the early 1940's in Altai preserve experiments were conducted for raising musk deer in captivity (A.G. Kostin).[31] Later, similar work was undertaken in Stolba preserve where about 12 animals were held in a nursery from 1951 to 1954. Offspring were raised successfully from two female deer. Experiments on live extraction of musk have not produced promising results (Shcherbakov, 1953; Dul'keit and Kozlov, 1958).

Musk deer are relatively rare in zoological parks. Methods of holding this animal in captivity have been studied little and captive animals usually die soon. In 1954 a small group of musk deer were transferred from Stolba preserve to Denezhkinsk Kamensk preserve in the Urals and set free for purposes of acclimatization. Tracks and deer were sighted there for at least a year but the experiment of acclimatization eventually proved positively unsuccessful. (A.N.)

---

[31] According to Solov'ev (1922) experiments on raising musk deer in captivity for obtaining musk in Ussuri region were conducted even before World War I. The correctness of this information is dubious.

TRUE OR PLESIOMETACARPAL DEER

Subfamily Cervinae Baird, 1857

Moderate to large-sized deer.

Toes four. Lateral toes usually relatively poorly developed but with phalanges. Only proximal part (plesiometacarpal extremities) of metacarpal bones retained; cuneiform distinct from naviculocuboid.

Facial part of lacrimal with distinct depression for preorbital gland. Orbital region of lacrimal with two tear ducts. Nasal process (pr. nasalis) of premaxillae does not reach frontal. Ethmoid pit large. Vomer relatively short and low at rear and does not separate choanae (posterior nares). Because of intense development of frontals, extending markedly backward, parietals greatly reduced. Apophyses of frontals, serving as base for antlers, relatively short and do not form ridges on frontals. Antlers invariably present (only in males) and relatively large. Fully developed antlers have more than two tines; first tine (brow tine) invariably developed but unbranched. Sometimes small flattened "spatula" occurs at tip of antlers.

Upper canine small, rudimentary, or absent. Dental formula:

$$i\,\frac{0}{3},\ c\,\frac{0-1}{1},\ pm\,\frac{3}{3},\ m\frac{3}{3}\ =\ 32 \text{ to } 34.$$

General build extremely slender and hind legs only insignificantly longer than forelegs. Tail moderately long or greatly reduced. 99 Naked portion at end of muzzle large. Toe cushions developed relatively poorly and occupy only roughly two-thirds of proximal part of hooves, projecting gradually forward into horny substance of hoof. Preorbital gland well developed. Metapodial glands present; sometimes significant gland clusters occur on tail; no musk or preputial gland present on abdomen nor any gland on outer surface of thigh. Glans penis without filiform protuberance. Preputial part of penis attached to abdominal skin. Gall bladder absent. Teats four.

Representatives of subfamily Cervinae are forest-steppe, forest, or montane forest forms, also found in swampy regions and in subalpine zones.

Cervinae represent a group of Old World deer. Only one species (*Cervus elaphus*) occurs in the New World and in North America is a relatively recent immigrant. In the Old World Cervinae are distributed in the south up to the limits of distribution of the family, and in the north roughly up to 55 to 60°N lat. (central parts of Norway and upper course of the Lena). In the New World they are found in North America roughly up to 60° N lat. on the north and 35° N lat. on the south (for details, see description of genus *Cervus* and red deer, *Cervus elaphus*, which follow).

Subfamily Cervinae in the area under consideration (described later) represent a well-defined, relatively monotypic group. These deer were placed in different taxonomic divisions by researchers for quite some time. Often *Elaphodus* and *Muntjacus*, and recently *Capreolus* and *Alces*, have been included in this plesiometacarpal group (Flerov, 1952). Group Cervinae may be considered a fairly natural group although its separation from Odocoileinae is based on relatively insignificant characters. Differences from Muntjacinae and Hydropotinae are more significant.

Cervinae are known from the Lower Pliocene of Europe and Asia; their occurrence in the Pliocene of North America has not been proved (relationship of the Upper Pliocene *Procoileus*, known from North America, to Cervinae not yet clear). Migration of Cervinae to North America probably took place in the Pliocene.

This subfamily, until very recently, was in an altogether unsatisfactory state from a taxonomic point of view. Concepts regarding the number, extent, and grouping of species were far from clear. First of all the number of species is very large and, secondly, special generic or subgeneric names have been assigned to almost all the well-defined species. Even forms which have been universally acknowledged as subspecies have been placed in different genera and subgenera. Various researchers hold various opinions. This is often true even now[32] but recent studies (Heptner and Tsalkin, 1947; Ellerman and Morrison-Scott, 1951; Flerov, 1952; Haltenorth and Trenze, 1956) have clarified the general picture and differences of opinion pertain to details, mainly number and extent of genera and subgenera. The number of species may be taken as established and changes are possible only in relation to some forms inhabiting southeastern Asia, primarily for downgrading them to the rank of subspecies.

---

[32] It is significant that the Siamese *Cervus schomburgki* (now probably totally extinct) has been regarded by some as a special subgenus (*Thaocervus*) of genus *Cervus* (Ellerman and Morrison-Scott, 1951). Others place it in the subgenus of barasingha (*C. duvauceli;* Haltenorth and Trenze, 1957).

The subfamily consists of eight genera (about 20% of all genera in the family) of which six are extinct and two extant[33] (about 16% of extant genera in the family). Extant genera are red deer (*Cervus*) and the Chinese or Pere David deer (*Elaphurus*). The remaining names proposed for species of the subfamily signify nothing more than their belonging to subgenera of genus *Cervus*. The total number of species is 15 or 16; genus *Elaphurus* is monotypic and the rest belong to genus *Cervus*. This number constitutes about 44% of the total number of species in the family.[34]

100 In the Soviet Union only one genus is found, red deer *Cervus* (50% of genera of the subfamily) with an autochthonous species (about 14% of the number of species in the subfamily).[35] Species of the subfamily comprise about 0.7% of the number of species present in Russian fauna.

In the Soviet Union Cervinae are found in the western part of the forest zone (western part of the region of broad-leaved forests), in the Crimea and the Caucasus, along the southern rim of the taiga, in Amur-Ussuri forests, and at places in Central Asia. In the last century, as a result of extinction, the geographic range shrunk at some places; as a result of acclimatization experiments from 1930 new sites of habitation have been created, partly within the old range and partly beyond it. Thanks to conservation measures implemented in the post-Revolution period, the deer population has increased in several places.

Cervinae are game and table animals and often objects of sport. In some parts of the range deer hunting is forbiddeen. (V.H.)

Genus of True Deer

Genus *Cervus* Linnaeus, 1758

1758. *Cervus* Linnaeus. *Systema Naturae,* 10th ed., vol. 1, p. 66. *Cervus elaphus* Linn. 1827. *Elaphus*. Hamilton Smith. Griffith's *Cuvier Anim. Kingdom,* vol. 5, p. 307. *Cervus elaphus* Linn.

---

[33] The number of fossil genera according to Simpson (1945); however he considers four extant.

[34] Pere David deer (*mi-lu* in Chinese) were found in the northeastern part of China proper (Hubeh, Shantung, and Henan) in prehistoric times and confined to flat marshy places. This deer became extinct (partly died as a result of the drying up of marshes) and before the commencement of the nineteenth century survived only in the palace gardens near Peking, from where it entered Europe. At present there are a few hundred living in parks in England (Woburn), Australia, and in zoological gardens.

[35] Fallow deer (*C. dama*), as an acclimatized species, have not been taken into consideration.

1838. *Harana.* Hodgson. *Ann. Mag. Nat. Hist.,* vol. 1, p. 154. *Cervus wallichi* Cuv.

1841. *Pseudocervus.* Hodgson. *Ann. Mag. Nat. Hist.,* vol. 1, p. 154. *Cervus wallichi* Cuv.

1846. *Strongylocerus.* Owen. *Brit. Fossil. Mamm. Birds,* p. 470. *Cervus elaphus* Linn.

1870. *Sika.* Sclater. *P.Z.S.L.,* p. 115. *Cervus sika* = *C. nippon* Temm.

1872. *Pseudaxis.* Gray. *Cat. Ruminants Brit. Mus.,* p. 70. *Cervus taiouanus* Blyth. (subspecies *C. nippon* Temm).

1874. *Elaphoceros.* Fitzinger. *Sitzungsber. d. Akad. d. Wissensch. Wien,* vol. 68, p. 347. *Cervus sika* Temm. = *C. nippon* Temm.

1898. *Sica.* Trouessart. *Cat. Mammalium,* p. 878 (substitute for *Sika* Sclater).

1898. *Sikaillus.* Heude. *Mém. Hist. Nat. Emp. Chin.,* vol. 4, p. 98. *Cervus sika* Temm. = *C. nippon* Temm.

1899. *Eucervus.* Acloque. *Faune de France, Mamm.,* p. 71. *Cervus elaphus* Linn.[36]

Cervus are plesiometacarpal deer of large, moderate, and small size.[37]

Skull relatively elongated and narrow, but fairly broad and short in some. Orbits relatively small, but fairly large in some.

Upper canine usually present in male, although very small, but absent in some; rare in female. Dental formula:

$$i\ \frac{0}{3},\ c\ \frac{0-1}{1},\ pm\ \frac{3}{3},\ m\ \frac{3}{3} = 32 \text{ to } 34.$$

Milk teeth moderate in height, sometimes with a fairly high and broad crown, but in some animals brachyodont. Sometimes an additional cusp occurs on upper molars on the inside.

Antlers vary in size from moderate to very large and are set some-
times at an acute angle; in some individuals highly inclined forward
or directed sideways. In number, size, and form of tines antlers
extremely diverse. Invariably first tine (brow tine) present and at
least two others. Number of tines on antlers usually 10 or a few
101 more.[38] Antlers invariably circular or oval in cross section; in one
case (*C. dama*) tip flattened into "spatula". In most (except *C. dama*
and the group *Rucervus*) tines set forward from main beam.

---

[36] Synonyms are given only for species inhabiting the Soviet Union.

[37] Height at shoulders ranges from 150 cm (maral) to 65 to 70 cm (Philippine deer, *C. philippensis alfredi*).

[38] In *C. schomburgki.* Individuals with 20 to 30 tines, found in some forms of red deer (*C. elaphus*), constitute an extremely rare exception.

Tail relatively short, of moderate length, or long (length may exceed ear length). Hind hooves covered by skin fold almost throughout their length. Preorbital gland large; it bulges in some individuals and is small in others. Metatarsal glands may be absent; if present, well developed, small, and either glabrous or with tuft of long hair. Short mane usually present on neck.[39]

Coloration of young deer spotted or uniform; in adults uniform or spotted in winter and summer. Speculum on posterior surface of rump varies in size and with or without dark border; sometimes totally absent. Black color along middle of tail absent with some exceptions. Female somewhat smaller and more slender than male.

Cervus undergo two molts every year.

There are forest, montane forest, and forest-steppe forms, but partly inhabit swamp forests.

The geographic range of the genus (reconstructed) is divided into two parts—American and Old World. In Africa the range covered the northwest, including Morocco, and probably extended up to the Spanish Sahara (northern parts of Rio de Oro).[40] In western Europe the range encompassed the western parts of England and Ireland, in the south the Mediterranean countries except Crete and Cyprus (Corsica and Sardinia fall in the range), and in the north the southern half of Norway and Sweden. In eastern Europe the northern boundary of the range traversed evidently along a line from Gulf of Riga, south of Moscow to the southern part of the central Urals, and in Asia from the central Urals to the northern banks of Baikal, central Lena and toward the Amur estuary. In the east the range encompassed the islands of Japan (including Ryukyu), Taiwan, Hainan, the Philippines (absent in Talaud group), Moluccan Islands, particularly Batian nd Dzhilolo (Halmahera; possibly acclimatized there from antiquity), Seram Islands, Timor, and Kambing adjoining Timor from the north (absent on Wetar), and the entire island complex north and west of the above places. On the Asian mainland the range of the genus covered Indochina, Malacca, Ceylon, India, Iran, Iraq, Asia Minor, Syrian region of the United

---

[39] In view of the diversity of form in the genus and the abundance of species, morphological characters are mainly those of Russian species.

[40] Information relating to distribution up to Senegal-Gambia inclusive (Lydekker, 1915) is dubious. Deer in small numbers are found at present only in the forest region at the border of Algeria and Tunisia. Information about Egypt is contradictory: according to some data fallow deer were acclimatized there even in antiquity, but according to other sources the animal was autochthonous there. Occurrence of *Dama schaeferi*, described recently for Egypt, is dubious.

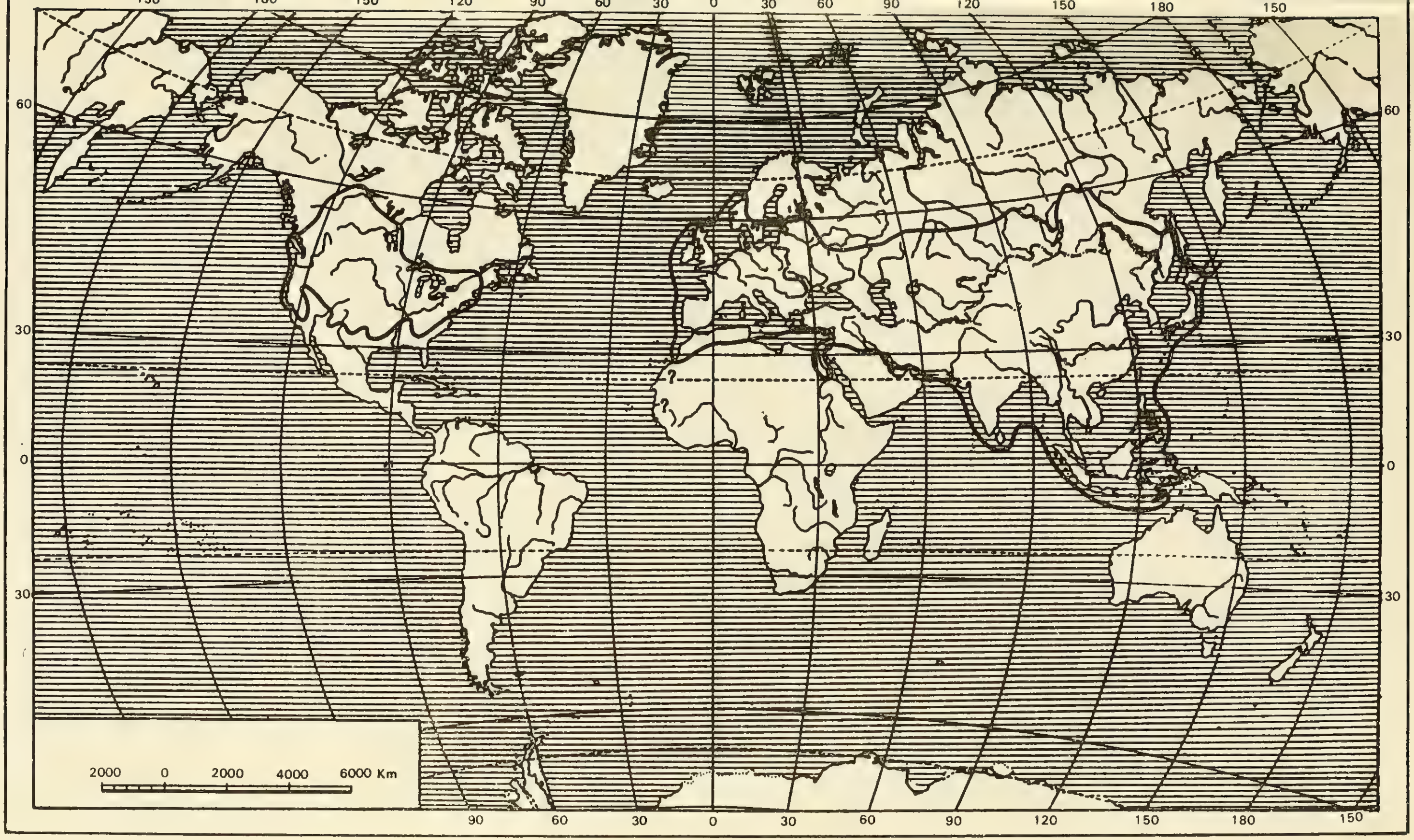

?
?
2000 0 2000 4000 6000 Km
60
30
0
30
90 60 30 0 30 60 90 120 150 180 150

Fig. 32. Geographic range (reconstructed) of subfamily of red or plesiometacarpal deer (Cervinae) and the genus *Cervus* L. Question marks relate to occurrence of red deer *Cervus elaphus* L. in Rio de Oro and Senegal-Gambia(scale in km). V.G. Heptner.

Arab Republic, Palestine, and the entire area up to the northern boundary in Siberia referred to above. In the New World the range covered North America roughly between 60° and 35° N lat. (for more details, see the section on red deer). From the range characteristics the genus should be regarded as Euro-Asiatic, associated largely with Asia, mostly its southern and southeastern parts.

Different forms of the genus are widely dispersed. Sambar were acclimatized in Bonin Island and Guam and then imported by local inhabitants even in the pre-European period into New Guinea, where they were originally absent. In the last decade deer (American and European forms of red deer, sambar, and spotted deer) have been acclimatized in New Zealand and South and North America. At several places in Europe deer had become extinct and their population was artificially restored later.

Genus *Cervus* in its characters and number of species occupies a central position in the subfamily. Genus *Elaphurus* (Pere David deer) is more isolated and exhibits no close generic association with genus *Cervus*.

Genus *Cervus* is known from the Middle Pliocene (or upper period of the Lower Pliocene; Flerov, 1950) of Asia. It evidently
103 prospered in southern Asia where, even at present, maximum diversity of species of the deer group *Axis*, known from the Lower Pliocene, is seen. The oldest forms of the genus belong to the group sambar (*Rusa*). In Europe representatives of the genus partly belong to its more primitive branches (type of sambar and sika deer, *C. nippon*), known from the Upper Pliocene. Deer migrated from Asia to North America only in the Pleistocene, where one of the Euro-Asiatic species (*C. elaphus*) has reached. In origin and in present distribution the genus should be considered predominantly south Asiatic.

The number of fossil species of the genus is quite large but all of them fall into extant groups within the genus. Some recent species can be traced to the Upper Pliocene in a relatively less altered state.

The taxonomy of the genus until recently was far from satisfactory. This is primarily true of the number of species, considered large even during the period when narrow concepts about species prevailed. The grouping of forms proposed and followed by various researchers was also extremely diverse and on the whole not really acceptable.

The genus consists of six subgenera: *Axis* (Indian spotted and "porcine" deer) with four species (*axis, porcinus, kuhli,* and *kalamianensis*); *Rusa* (sambars of southern Asia and Australia) with four species (*unicolor, equinus, timorensis,* and *philippinus*); *Przevals-*

kium (Tibetan white-breasted* deer) with one species (*albirostris*); *Dama* (fallow) with one species (dama—*D. mesopotamica,* a subspecies of *C. dama*); *Rucervus* (barasingha or swamp deer of Indochina and India) with two or three species (*eldi, duvauceli,* and *schomburgki,* the last evidently only a subspecies of the second); and *Cervus* s. str. (red deer) with two species (*elaphus* and *nippon*). Other subgenera have also been isolated (*Panolia, Sika, Taocervus,* and *Hyelaphus*), but such a division is superfluous (proximate species in such a division often fall in different subgenera). During the period of extreme division even well-defined races of the same species (*C. elaphus*) were placed in different subgenera. It is highly probable that subgenus *Przevalskium,* and probably also *Rucervus,* should be placed among *Cervus* s. str. and only four subgenera recognized.

In toto the genus comprises 13 or 14 species or about 93% of species of the subfamily. Of these, 12 or 13 are purely Asiatic and one (*C. elaphus*) occurs mostly in Asia, but is also found in American, European, and African parts of the range of the genus.

These are game and table animals caught for their meat, hide, and antlers in velvet. At places they represent the main object of regulated hunting. Hunting of species which are few in number is prohibited. *C. schomburgki* is extinct (Siam).

Two species are found in Russian fauna—spotted [sika] deer (*C. nippon* Temm., 1937) and red deer (*C. elaphus* Linn., 1758)—representing 14 or 15% of species of the genus and constituting 0.7% of species of Russian fauna (mammals).

These two species are inhabitants of deciduous and mixed forests in the west European part of the USSR, the Caucasus, southern fringe of the taiga, mountain forests of southern Siberia, and central Asian tugais [vegetation-covered bottomlands].

These are mainly game and table animals, the hunting of which is often banned. At places they are raised in a semidomesticated state for purposes of obtaining antlers in velvet. (V.H.)

3. SPOTTED [SIKA] DEER

Cervus (Cervus) nippon Temmink, 1838[41]

1838. *Cervus nippon.* Temmink. *Coup d'oeil sur la fauna des iles de la Sonde et de l'Empire de Japon,* p. 22. Japan.

---

*Error in Russian original; should read white-lipped.

[41] In Soviet literature the following names are common for these deer according to sex and age: male—"olen' " [buck], female—"olenukha" [doe], and young two-year-old male with simple unbranched antlers ("saek," "saenysh," or "shil'nik").

1845. *Cervus sika.* Temmink. *Fauna japonica, Mamm.*, p. 54, fig. 17. Japan.
1861. *Cervus pseudaxis.* Gray. *Proc. Zool. Soc., London,* p. 236.
1864. *Cervus hortulorum.* Swinhoe. Ibid., p. 169. Park of Summer Palace near Peking. True native place of these animals is Manchuria.
1864. *Cervus mantchuricus.* Swinhoe. Ibid., p. 169.
1876. *Cervus dybowskii.* Taczanovski. Ibid., p. 123. Southern part of Ussuri region.
1899. *Cervus mantschuricus major.* Noack. *Humboldt,* vol. 3, p. 9. Suifun, Ussuri region (?).
1910. *Cervus hortulorum typicus.* Ward. *Rec. Big Game,* 6th ed., p. 52. Manchuria.[42]

Diagnosis

Summer fur of animals of all ages spotted (in winter the spots are poorly visible or not developed at all). Speculum very small and does not extend above caudal base on croup. Antlers usually with no more than four tines each. Tail long, almost equal or equal to length of ear. Height at withers not more than 112 cm. (V.H.)

Description

Animals of moderate size, very slender and elegant, and the most slender of all Russian deer. Neck long, almost vertical, and head held high. Croup slightly higher than withers. Ears relatively short, proportional. Tail relatively long and equal or almost equal to ear length.

Antlers slender, relatively light, small, set very straight, and tips fairly close-set. Beam circular in cross section. Tines on full antler four: one brow (bez tine absent), one central, and two terminal set in sagittal plane. Crown usually not developed but sometimes third terminal tine seen exceptionally in old and particularly powerful

---

[42] Apart from these actual synonyms for Ussuri forms Soviet literature also uses the names *C. dama* and *C. axis* for sika deer. In actual fact *C. axis* refers to the Indian species.

animals, forming an incipient crown.[43] Sometimes rudimentary bez tine present, i.e., six tines. The latter, however, is an abnormality and the antlers under these conditions generally exhibit features of irregular development. In very old animals, especially those with additional tines, the clearance between antlers (distance between terminal parts of the beam) is more, even extraordinarily—almost as
105 much as in European deer. Color of antlers dark brown; tips of tines in well-developed antlers smooth and yellowish-white.

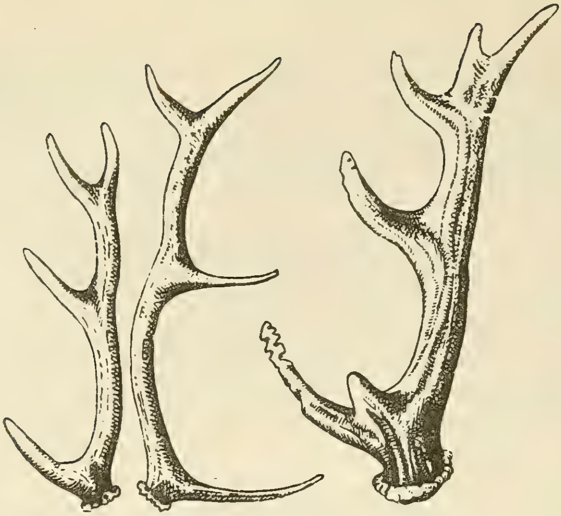
Individual color variability is fairly high with regard to general color of fur and number, disposition, and color of spots. The main shade of fur in type forms is rusty. Along the spine the fur is somewhat darker, becoming lighter (ocherous and dirty white) along the bottom on the sides and on the back. The rusty color extends onto the legs also where, however, it is pale. The neck and underbelly are pale yellow or dirty gray and the head pale brown. A dark band runs from the occiput along the neck and back, disappears on the sacrum, appears again at the caudal base, and extends right up to its end. A pale yellow band forks off the dark band of the tail on each side. The tail at the base is bare. Downward and to the side, from the caudal base to the rear of the thigh, a triangular speculum of white hair forms. It points downward and merges with the white color of the inside of the thighs and inguinal region. The speculum is extremely small and bounded on top by a dark band. The hair on the speculum is somewhat longer than on the trunk, reaching 2.5 to 3.0 cm in length*; this hair stands on end when the animal is frightened.

Against the main rusty background on the trunk scattered, pure white, distinct spots occur. They are smaller on the back and gradually enlarge toward the abdomen. On the sides of the body the spots fuse here and there and form white longitudinal bands of up to 10 cm in length. The arrangement of spots shows distinct individual variations but two discontinuous rows are generally seen on both sides of the spine and one each on the sides. The coat of males differs from that of females in that the hair on the head is dark gray, with brown and longer hair on the neck and throat.

---

[43] Such antlers are not seen at present (Bromlei, 1956). Formerly, when there were many animals, deer with antlers with five tines were evidently encountered more often in taiga (Menard, 1930). The report about 15-year-old animals in Hagenbeck Zoological Garden (brought while young from Sidema Park near Vladivostok) with 10 tines and antlers not inferior in power and beauty to those of German deer (Menard, 1930) appears dubious. In any case this is an abnormal, exceptional phenomenon.

*Some confusion with regard to length of hair on the speculum occurs in the text. Contradiction is apparent two paragraphs later—General Editor.



104 Fig. 33. Antlers of wild sika deer (*C. n. hortulorum*) from Ussuri region 3.5, over 4, and 10 to 12 years old.

The general hue of the winter coat of females is grayish-brown, the head light dirty gray, and the inside of the ear pale gray. Along the back runs a faintly discernible dark brown band which enlarges toward the rear. The central portion of the tail toward the base is dark brown and white along the sides. On the hind quarters occurs a small white speculum bounded on the upper side by a dark brown band which fuses with the band on the back. The legs are grayish-brown, darker in front and much lighter behind. The inguinal region and upper inner surface of the legs are whitish, and the lower part of the chest dirty brown. Light-colored spots occur on the back, upper portions of the sides, thighs, and shoulders. Their number in winter is significantly less than in summer and the outlines are not sharp. Spots are not seen in all adult animals and, moreover, by spring, because of wear of the fur often disappear even in those individuals in which they were apparent from autumn. Hair length on the trunk, 5 to 7 cm.

Long dark hair grows in the form of a small mane on the neck and nape in the winter coat of males; this is not so in females. Males have much darker hair on the chest and along the middle of the belly (in the preputial region). In some animals the entire fur is uniformly rusty in coloration but darkening (to deep brown) of the neck hair has also been recorded.[44]

---

[44] This description comes from Bromlei (1956) and pertains to wild animals (not held in zoological gardens).

Young animals in their first summer coat are very similar to adults but their spots are larger and also occur along the middle of the back and on the sides. In their first winter coat spots are often present and usually well defined.

Preorbital glands are well developed. Tarsal glands are oval, elongated, and covered with bristly hair which is much longer than the surrounding hair and much lighter in color.

The skull is typical of the genus and subgenus *Cervus* and very similar to that of red deer (*C. elaphus*). Differences in sika deer, apart from overall small size, include considerable enlargement of the cavity of the typanic bullae, which is convex and rounded, without ridges and crests on the surface. The corresponding parts in red deer are not enlarged but narrow, and the bullae relatively slightly convex and angular (Flerov, 1952).

106 Males and females attain full growth and weight by the third year. The size of animals three years old and older are as follows:

Males (five specimens): body length from tip of muzzle to anus 168 to 180 cm (M 173); height at withers 104 to 112 cm (M 109); chest circumference 114 to 130 cm (M 122); distance of hind hoof from hock 47 to 52 cm (M 50); tail length without end hair 17 to 19 cm (M 18); length of ears 17 to 20 cm (M 18.6); weight 104 to 131 kg (M 117.4).

Females (12 specimens): body length 149 to 174 cm (M 162); height at withers 87 to 98 cm (M 94); chest circumference 96 to 112 cm (M 104); length of hind sole 44 to 49 cm (M 46); tail length without end hair 14 to 17 cm (M 16.3); length of ears 16 to 18 cm (M 17); weight 60 to 83.7 kg (M 73.1).

The length of antlers of adult animals (with four tines) varies from 65 to 79 cm and weight from 810 to 1,260 g (eight specimens). An exceptional antler of a very old animal with six tines weighed 1,887 g.[45] Antlers of wild deer are known to reach 90 to 93 cm in length (Menard, 1930). The maximum skull length is 320 cm.

In captivity sika deer interbreed readily with Manchurian wapiti. Formerly, when sika deer were abundant in the taiga, such hybrids were found so frequently in nature that they had a special Chinese name.[46] Hybrids are intermediate in size between parent species, but in general resemble sika deer more. Their fur in summer is spotted but the spots are yellow, not white, and less sharp. The antlers and tail resemble those of sika. The crossing of a male sika with a female Manchurian wapiti in a nursery invariably yields rust-colored offspring without spots, similar to the female parent. Such forms are not encountered in nature (Menard, 1930). (V.H.)

---

[45] All the morphometric data pertain to wild deer and are taken from Bromlei (1956).

[46] Sika deer are called "hua lu" ("flower deer"), Manchurian wapiti "ma-lu," and their hybrids "chin-da-guiza". Antlers in velvet also differ in these forms. According to Bromlei (1956), contrary to many other authors, the crossing of these species in nature was a very rare phenomenon in the past. No doubt this remains true even today.

Taxonomy

Within the genus *Cervus* the subgenus *Cervus,* accepted here in a broad sense, represents the most specialized and progressive group. The evolutionary sequence of specialization proceeds as follows: from *Axis* to *Rusa, Rucervus,* and *Przevalskium.* Only in external characters are Russian sika similar to Axis deer (Indian spotted deer) with their permanent bright spotted coloration (in the past some researchers regarded and labeled the former Axis deer). Apart from several osteological characters, the former differ from the latter in the structure of the antlers; in Axis deer they invariably have three tines (intermediate forms absent).

Within the subgenus sika represent a more primitive form than *C. elaphus.* This is borne out by the simpler structure of antlers (four tines, absence of bez tine and crown) and spotted coloration in adults. Yet the two species are undeniably quite close. Among its extremely diversified races *C. elaphus* has forms without a bez tine, or without a crown, and also forms in which spotted coloration of the summer coat is not at all uncommon as an individual aberration, or even usually present. Finally, some forms of this species are no larger than sika deer. The close affinity of these two species is underscored by their relatively frequent hybridization in nature. In captivity they freely interbreed in all combinations. (V.H.)

Geographic Distribution

These animals range over eastern Asia from the Ussuri region to southern China and northern Vietnam and some of the adjoining islands.

107 *Geographic Range in the Soviet Union*

The range in the Soviet Union comprises the extreme northeastern rim of the range of the species and occupies a very small territory in the extreme south of the Far East.

The northern boundary of the range (reconstructed) is not fully

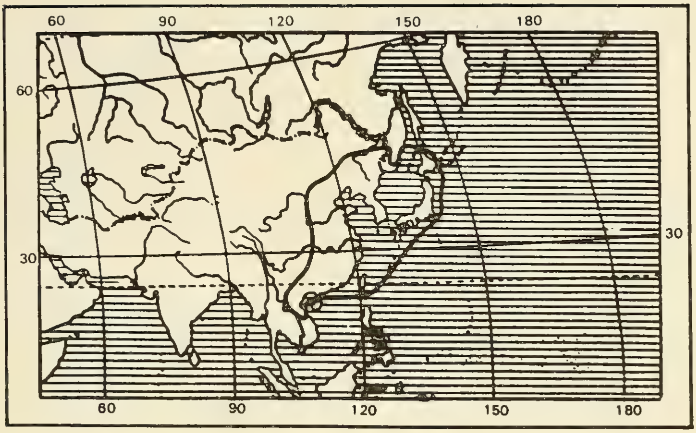


Fig. 34. Reconstructed geographic range of species of sika deer (*Cervus nippon* Temm.). V.G. Heptner.

known. In the Ussuri valley and the western slopes of Sikhote-Alin mountains adjoining it the boundary extended almost up to the Bikin estuary (Maak, 1861),[47] i.e., roughly along 47°.

The northernmost habitation of these deer on the eastern slope of Sikhote-Alin mountains is 46°00′ (Abramov, 1928). Evidently these deer penetrated a few tens of kilometers in the north (Khutsin; Bromlei, 1956). The position of the boundary between these two points has not been established but there is no doubt that along Sikhote-Alin it curved strongly southward; deer were absent in the middle altitudes of the region. South of the above line deer were seen everywhere, including all the islands of Peter the Great Bay. The range extended beyond the boundaries of the Soviet Union in the south (into the Korean Peninsula) as well as to the west (into Manchuria).

During the last century the range shrank notably and the northern boundary withdrew southward, at places very considerably. The

---

[47] These deer normally inhabit regions up to Iman; seen very rarely north of it, transgressions from the south were recorded every year (Maak, 1861; Przewalski, 1870). The extreme northern places of deer sightings were Bikhark mountains and the Diongo mountain chain (Maak, 1861) on the right bank of the Ussuri, slightly below present Nizhne-Mikhailov village on the Ussuri above the Bikin estuary. The northernmost transgression occurred at Khat, slightly above Nora estuary on Ussuri (Maak, 1861). This location fell in the present-day Vidnoe village on Ussuri, below Bikinsk estuary and above Neolikha estuary (Nora), dropping into Ussuri on the left.

In Bromlei's book (1956) the boundary according to data from Maak (1861) has been reconstructed incorrectly and cannot be properly deciphered.

108 main reasons for changes in the range were the extermination of animals by hunters and changes in topography. In recent years wolves have come to play an important role (see below). Currently the range (taking into consideration the occurrence of individual animals and small groups as well as transgressions) encompasses the far south of the Ussuri region, roughly up to 44° N lat. On the eastern slopes of Sikhote-Alin, in the region adjoining the sea, the range runs farther north. It extends as a narrow band northward up to Sikhote-Alin preserve and Khuntuez Bay (Abramov, 1954; G.F. Bromlei), i.e., roughly up to 45°20′–30′. The animals evidently reached even up to 46°. In this section no significant changes in the boundary occurred during the last century.

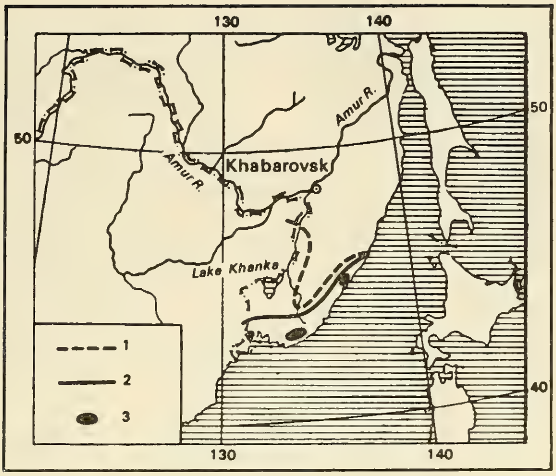
Apart from a general withdrawal to the south, range reduction was also evident in its division into several fairly isolated sections. The number of such sections (and also the number of animals in them) dropped rapidly and their isolation became complete. By 1950 there were three such totally isolated sections on the mainland—
109 Kedrovaya Pad' preserve (from the western bank of the Amur Gulf to west of Vladivostok), region of the former Sudzukhin preserve along the Sudzukh River to east of Suchansk, and Sikhote-Alin preserve. The number of animals in all these places is very small, not exceeding a few dozen (G.F. Bromlei).[48]

Deer are also present on islands in Peter the Great Bay—Askol'de, Putyatine, Rikord, and Rimsk-Korsakov (Abramov, 1954). These animals are descendants of wild deer but lead a semidomesticated life (for velvet antler recovery). Animals have not survived on the rest of the islands.

Commencing from 1937 a small number of deer, taken from farms, were transferred to some preserves for purposes of acclimatization (Fig. 36). Deer were colonized in Il'men preserve (southwest of Chelyabinsk), Buzuluk (near Buzuluk), Kuibyshev preserve in Zhigulyakh, Mordov (southwest of Arzamas near Temnikov), Oka preserve (along the Pre River east of Ryazan'), Khoper (on the Khoper River near Borisogleb), and Teberdin preserve (in the northern Caucasus on the Teberda River, tributary of the Kuban). There are no deer at present in the territory of Kuibyshev preserve but they continue to survive in other places of acclimatization. Deer did not settle outside these sanctuaries or were present in extremely insignificant numbers.

---

[48] Deer detected in the upper courses of the Imansk around Sidatunsk village evidently represent escaped domesticated animals (G.F. Bromlei).



107 Fig. 35. Distribution of sika deer (*Cervus nippon* Temm.) in the Soviet Union. 1—reconstructed northern boundary circa 1850; 2—boundary of range in last decade of nineteeth century and early present century; 3—recent (1940's and 1950's) habitats in Kedrovaya Pad', Sudzukhin, and Sikhote-Alin preserves. V.G. Heptner.

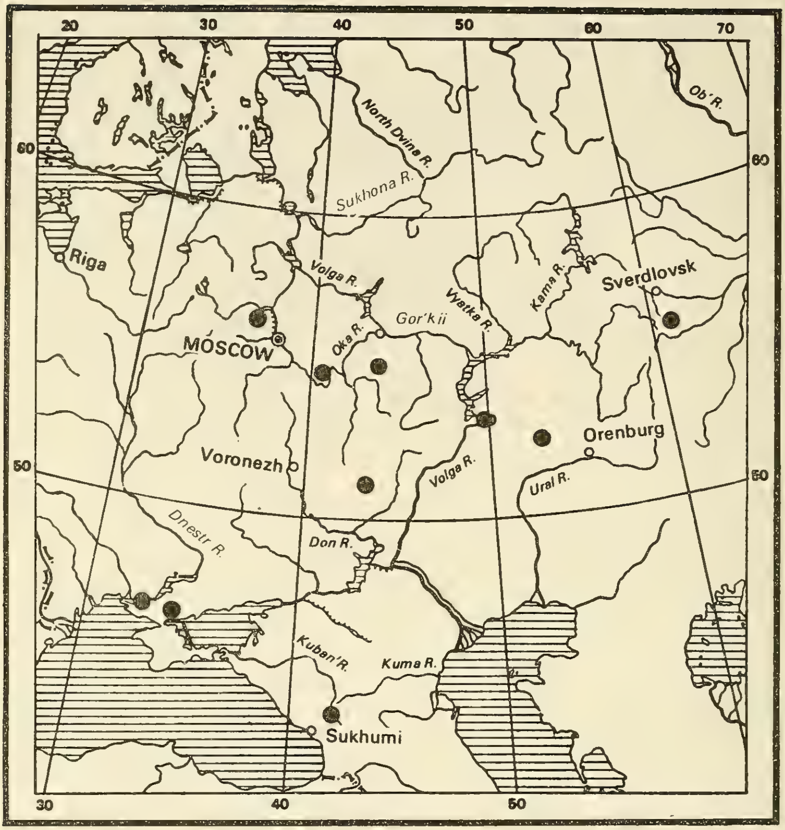
Apart from the places listed above, deer have also been taken to Azerbaidzhan, Armenia, and several times to different places in Moscow district, around Vil'nyus, and some other areas. Such transfers were made by hunting organizations and the results are not yet definitive but so far hardly encouraging. Deer have likewise been imported into Borkuta in the floodplain of the lower course of the Dnieper and into several game farms of the Ukraine. These animals originated from Askaniya-Nova (for details, see below).

Geographic Range outside the Soviet Union

The range outside the Soviet Union covers the eastern part of northeastern China—the mountain region adjoining the Ussuri region and Korea,[49] part of the Sungari basin, Korea, and much of eastern and southeastern China. In the west the range includes southern parts of Jehol and western parts of Shansi, i.e., up to the meridianal course of the Hwang Ho, Henan, Hupeh, and Kwangsi. In the east the range extends up to the sea (specifically, it covers Shandong,

---

[49] Chzhan-Guan-Tsailin, Khentei-Alin, and Van-Lun-Gou mountains (Baikov, 1915).


20
30
40
50
60
70
60
60
North Dvina R.
Ob' R.
Sukhona R.
Riga
Volga R.
Sverdlovsk
Kama R.
Vyatka R.
Gor'kii
Oka R.
MOSCOW
Orenburg
Voronezh
50
50
Volga R.
Ural R.
Dnestr R.
Don R.
Kuban' R.
Kuma R.
Sukhumi
30
40
50

108 Fig. 36. Some points of acclimatization of sika deer (*Cervus nippon hortulorum*) in the European part of the USSR, Urals, and the Caucasus (there are no deer at present in Kuibyshev preserve on Samarsk Luka). V.G. Heptner.

Cheking, Fukien, and Kwangtung provinces). Farther away in the south the range extends into northern Vietnam (Tonking province, or Bakbo and Annam or Trunbo).

Cheju-do (Qvelpart), Tsushima, Honshu, Hokkaido, Shikoku, Kyushyu, Yakushima, Ryukyu, and Taiwan Islands fall within the range.

Over the greater part of China deer are totally extinct or extremely rare (in northeastern China and in the south they are still seen but few in number).

Sika deer, particularly the Ussuri form, have been successfully acclimatized in New Zealand. (V.H.)

Geographic Variation

The geographic variability of the species is slight within its relatively small range. A well-defined form inhabits the Soviet Union.

Ussuri sika deer, *C. (C.) n. hortulorum* Swinhoe, 1864 (syn. *mantschuricus, mantschuricus major, dybowskii,* and *hortulorum typicus*), is the largest form of the species (for description, see above). Its range covers the Ussuri region.

Outside the Soviet Union Ussuri sika deer are found in northeastern China, Korea, and evidently the entire northern half of China (in the south up to the Hwang Ho).

Three forms are distinguished outside the USSR: *C. n. kopschi* Swinhoe, 1873 (from the Hwang Ho to the southern boundary of the range) is close to the Manchurian form and as large; *C. n. nippon* Temm., 1838 (islands of Japan including probably Ryukyu) is probably a distinct form characterized by very small size (height at shoulders about 95 cm); and *C. n. taiouanus* Blyth, 1860 (Taiwan).

110 Some researchers distinguish up to nine forms of sika deer (in addition to those listed above: *mantschuricus, mandarinus, grassianus,* and *pseudaxis* from the mainland and *keramae* from parts of Ryukyu archipelago). Such distinctions are positively incorrect. At the same time a thorough analysis of geographic variability is presently impossible since old descriptions are of little use, while new material is inaccessible since deer are extinct in much of the range of the species on the mainland. Theoretical concepts contravene recognizing a large number of races on the mainland. In any case Ussuri deer do not differ from Manchurian deer.

Some earlier researchers (Przewalski, 1870; Maak, 1861) affirmed two species of sika deer in the Ussuri region. Such statements are based partly on an improper evaluation of individual variability, mainly in relation to the presence in the region of hybrids of this species and Manchurian wapiti (discussed above). That this is so is evident from the Chinese nomenclature cited by Maak (1861). (V.H.)

Biology

Population. Over the last 80 to 100 years the population of wild sika deer in the Soviet Union decreased several times, mainly as a result of their extermination by hunters in pre-Revolutionary Russia, especially during snowy winters, for example in the winters of 1877 to 1878 and 1914 to 1915 (Yankovskii, 1882; Bromlei, 1956). At the end of the 1880's in the Far East the first antler farm based on sika deer was established. Such farms were initially filled with captured animals and often poorly organized, leading to deer mortality. Finally, the gradual clearing of Primor'e forests, establishment of new villages, the appearance of a large number of wolves and hunting dogs, and other factors also led to a reduction in the population of these wild ungulates.

How greatly the population of sika deer decreased in the Far East can be judged from indirect indexes like changes in herd size. In the 1860's and 1870's herds of 20 to 30 or even 40 to 50 animals were often sighted (Przewalski, 1870; Yankovskii, 1882). A group of 14 deer has been observed only once throughout the existence of Sudzukhin preserve (up to 1951), representing the main reserve of wild sika deer in the Soviet Union; all the remaining herds are no more than six or seven, and more often three or four strong (Bromlei, 1956).

Abramov (1930) estimated the number of wild sika deer at the end of the 1920's in the Far East at 900 to 1,100 (800 to 1,000 in the former Vladivostok region and up to 100 in Khabarovsk). In 1949 they did not exceed 300 (Bromlei, 1956), of which 160 were in the territory of Sudzukhin preserve, 20 in Sikhote-Alin, 30 each in Suputinsk and Kedrovaya Pad', and 60 outside the preserves. After Sudzukhin preserve was closed down in 1951 the number of wild sika deer decreased further.[50]

In 1938 a total of 240 sika deer were transferred from Far East reindeer farms to Il'men preserve (Trans-Urals) and other sanctuaries in the European part of the USSR and set free. They have flourished and at places penetrated into regions adjoining the preserves (not more than several tens of kilometers from the points of release) but their number has only doubled as of now. In most of the new regions the snow cover has proved too severe for their survival. In 1953 to 1954 in these preserves and adjacent areas sika deer numbered as follows: Teberdin—21 to 36, Khoper—206 to 209,[51] Oka—70
111 to 99, Mordov—151, Il'men—20 to 35, and Kuibyshev preserve and Buzuluk Bor a few solitary animals, i.e., a total of 500 deer. Maximum population growth has been seen in Khoper (7 to 10 times), Oka (3.5 times), and Mordov (2.5 times) preserves. In the other preserves the number of deer did not increase or, in fact, decreased (Il'ina, 1956). In Teberdin preserve deer had almost totally disappeared by 1956; at present, they are found only outside the preserve, in the much lower parts of Karachai autonomous region (Arens, 1957;

---

[50] In 1957 the preserve was reopened.

[51] Up to 300 deer were counted in 1955 in Khoper preserve and neighboring forests (D'yakov and Aleinikov, 1956). This figure appears somewhat inflated.

Inyakova, 1957). In Kuibyshev preserve sika deer have disappeared altogether (I.V. Zharkov).

Small numbers of sika deer were brought into different regions of Moscow district between 1933 and 1955: 6 animals were released in 1952 in Khuzinsk region of Azerbaidzhan Soviet Socialist Republic, and 20 in 1953 in Vedinsk region of Armenian Soviet Socialist Republic (Il'ina, 1956). As early as 1909 sika deer were imported into Askaniya-Nova where they are present even today. In 1941 about 80 deer were set free in the Dnieper division of Askaniya-Nova preserve at Borkuta; deer in the Dnieper floodplain (on the left bank) have multiplied and their number now is appreciably greater (Salganskii, 1952). In 1956 over 100 deer were imported from Askaniya-Nova into game farms in the Ukraine. Deer have also been set free in the region of Black Sea preserve. Recently sika deer (24 animals from Altai state farm) were released near Kaunas (Lithuanian Soviet Socialist Republic) and in 1955 produced offspring (Ivanauskas, 1957).

For the Soviet Union as a whole the population of wild sika deer is probably 1,000 or more.

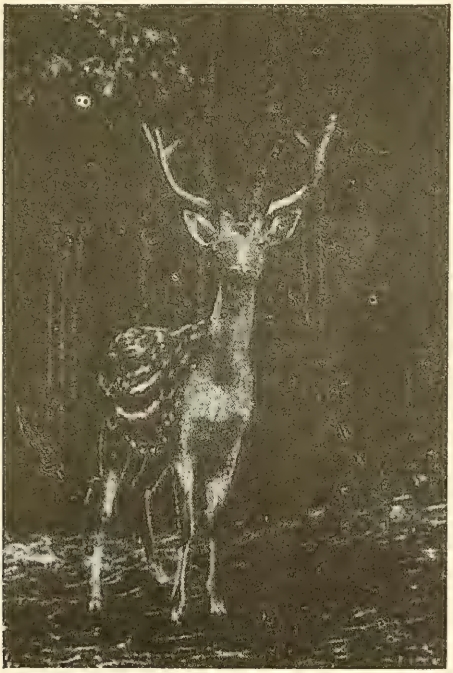


Fig. 37. Sika deer in summer coat. Il'men preserve. Photograph by N.N. Nemnonov.

Habitat. In the Primor'e region sika deer inhabit mainly broad-leaved oak forests of the Manchurian type and rich undergrowths, are rarely seen in mixed nut pine-broad-leaved forests (usually not above 500 m), and do not penetrate nut pine-conifer taiga; they avidly feed in growing burned-over forests. Sika deer find best conditions at places where the total winter precipitation in the form of snow does not exceed 800 to 1,000 mm, the first snowfall commences relatively late, the total number of days with snow cover averages less than 45, and the height of the snow usually does not exceed 25 to 30 cm. Of particular interest to deer are the southern and southeastern slopes of mountain ranges along the sea, where the snow cover usually does not last longer than five to eight consecutive days since it is soon washed away by rains. Preferred habitats are those with rugged topography and abundant streams. Females and young deer are found in large numbers slightly lower on slopes and closer to the sea compared to adult males (Abramov, 1929 and 1939; Bromlei, 1959).

Sika deer released in Trans-Urals and the European part of the USSR find conditions there incomparably more difficult in winter, 112 as the snow cover persists for up to 150 days (Il'men preserve), its height often exceeds 60 cm (Il'men and Mordov preserves, Zhiguli, and Buzuluk Bor), and minimum temperature at some places (Buzuluk Bor) reaches –49.5°C (Arsen'ev, 1949). Deer in these regions are confined mainly to deciduous and mixed forests; in winter in Il'men and Oka preserves, when the snow is deep, they are usually confined to pine groves (Il'ina, 1956). In Teberdin preserve sika deer sometimes penetrate to a height of 1,600 to 1,700 m, which is not characteristic of deer in the Primor'e region.

Food. In the Primor'e region wild sika consume no less than 129 plant species. Trees and shrubs play the most important role, especially in summer; their proportion in the diet of deer reaches 70% (by volume) (Bromlei, 1956). Among the main food items are acorns, leaves, buds and slender branches,[52] oak shoots, Manchurian aralia, and lime. Lespedeza, acanthopanax, Amur zovk, Manchurian nuts, and Amur grapes are also preferred items. In spring elm, maple, ash, and sedge, and in summer umbelliferous and other plants become dietary items. Deer gnaw tree barks other than oak (which is totally inedible) mainly in the second half of winter when the snow is heavy. Under very similar conditions branches of willow, bird cherry, and alder also serve as food. Deer feed on acorns in winter and continue to dig them up from under snow up to 30 cm deep and when the acorns are abundant, even when the snow is 40 to 50 cm thick. They feed well not only on green but also on dry oak leaves clinging to branches as well as those which have dropped if they are not rotten. Deer dig up leaves from under the snow. On the sea coast they look for eel grass and laminaria, attracted by their saltiness; deer usually consume them only in winter and simply chew them in summer. Unlike other ungulates these deer usually feed poorly on grassy substances and arboreal lichens[53] (Vendland, 1938; Bromlei, 1956).

---

[52] Manchurian wapiti consume thicker branches as they have a thickened skin on the lips; sika deer have no such thickened skin (Bromlei, 1956).

In preserves in the European part of the USSR and in Trans-Urals sika deer consume over 390 varieties of plants, of which only about one-eighth are the same as those eaten in the Primor'e region; 15 species are consumed avidly and 173 well. Some species of plants consumed well in preserves in the European part of the USSR and Trans-Urals are poorly consumed in the Primor'e region and vice versa. Compared to the Primor'e region, the role of forest shrubs in the summer diet is significantly less; deer at this time of year feed mainly on tall grasses (Il'ina, 1956).

In Il'men preserve the consumption of 143 plant species has been recorded (Averin and Ushkov, 1947), in Mordov—36 plant species (K.N. Nikitin), Khoper—132 (D'yakov and Aleinikov, 1956), Kuibyshev—154 (A.N. Goncharova; and others), farms of Buzuluk Bor—80 (Darkshevich, 1939), and around Moscow—63 (Matyushin, 1954). In the Kuibyshev preserve steppe regions where deer have settled (Zhiguli) they consume in early spring 110, in winter 60, in summer 55, and in autumn 34 plant species. Warty barked spindle tree [*Euonynus verrucosus*], maple, rowan, oak, pine shoots, etc. are consumed more avidly than others (A.N. Goncharova). In Teberdin preserve acorns and beechnuts are well consumed (when available, deer dig them up from under snow 50 to 60 cm thick) and branches of hazel, oak, aspen, willow, elm, and especially spindle tree. Those of special interest from among herbaceous plants are cow parsnip, spirea, lady's mantle, cinquefoil, etc. (Kurapova and Stepanov, 1940; Knyazev, 1946). In Oka preserve in winter deer feed mainly on the branches of willow, brittle buckthorn, oak, and aspen (Il'ina, 1956). In Il'men and Mordov preserves, when the snow is 30 cm thick, deer almost totally consume hay from places of cattle grazing and stocks dropped accidentally on the roadside. When food is inadequate
113 hungry deer in Mordov preserve consume large quantities of young

---

[53] In farms around Moscow and in Khoper preserve wild deer take well to arboreal lichens (Matyushin, 1954; D'yakov and Aleinikov, 1956).

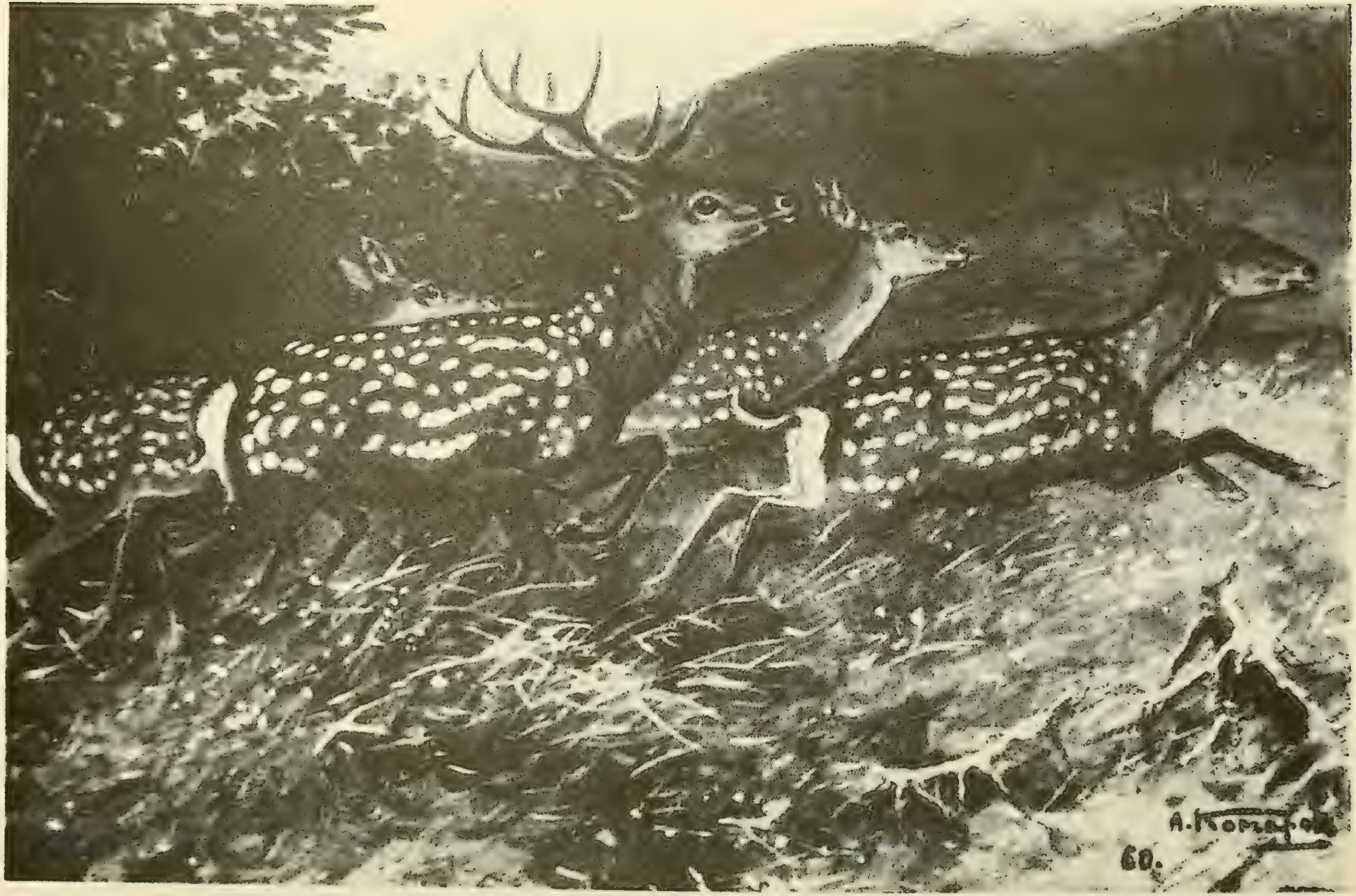

А.Комаров
60.

Plate I. Sika deer, *Cervus (Cervus) nippon* Temm., in summer coat. Drawing by A.N. Komarov.

pine shoots and gnaw at pine and spruce bark (P.M. Reshetnikov; F.D. Shaposhnikov; and others).

In Suifunsk deer farm domesticated sika deer consume 179 plant species from 37 families (of the total number of 364 species of forest plants in southern Primor'e), including trees, shrubs, herbage, legumes, grasses, aspen, horsetail, and ferns. Oak, lime, and briar (*Smilax*) are more avidly consumed, 52 species consumed well, and 72 satisfactorily. Among the plants consumed are aromatics with a pungent smell and those which are poisonous to cattle (Ryabova and Saverkin, 1937). Thus the stenophagy and poor adaptability of sika deer in food selection reported by some researchers is not confirmed.

A sika male weighing 100 kg requires 2.0 kg food containing 0.20 to 0.25 kg digestible proteins per day, while adult females of different ages require 1.6 to 2.4 kg food containing 0.14 to 0.22 kg digestible proteins (Mirolyubov and Ryashchenko, 1948).

Deer visit some warm mineral springs and sometimes drink sea water. In search of mineral matter they lick algae and other marine materials washed ashore (holothurians, pebbles, etc.) and also ashes (Bromlei, 1956). Deer visit artificial salt licks only in some regions

Fig. 38. Herd of sika deer in Maikha state farm. Primor'e region, 1953. Photograph by N.N. Nemnonov.

where they have been acclimatized.

Home range. Some lone animals and herds of sika deer have their own home range, the size of which for lone animals rarely exceeds 100 to 200 hectares. In the period of rut a male with four or five females is confined to an area of about 400 hectares, and a much larger herd (14 to 16 animals) to a region of 800 to 900 hectares (Bromlei, 1956). In winter in Primor'e region, especially when the snow cover is very thick, many deer survive for weeks in an area comprising several tens of hectares or even smaller, for example, wandering along unfrozen streams and feeding on trees along the banks. In winter the daily wandering of deer in Sudzukhin preserve often exceeds 300 m (G.F. Bromlei); in Mordov preserve when the snow cover is about 50 cm deep wandering averages 1,500 m for a male,
114 but only 500 m when the animal feeds on hay (F.D. Shaposhnikov). In Oka preserve, when the snow is not more than 30 cm thick, daily travel does not exceed 2.0 to 2.5 km; when the snow is very thick or has a frozen crust daily travel is limited to 0.6 to 1.5 km (Il'ina, 1956).

In the total area of 339,000 hectares of Sudzukhin preserve, sika have been sighted in summer only in 42,000 hectares and in winter in 15,000 hectares. In summer, depending on the total population of sika deer in the preserve, their density has varied in different years from 3.5 to 12 animals per 1,000 hectares; density is higher in winter. This value under conditions of Primor'e region is closer to maximum for the species (Bromlei, 1956).

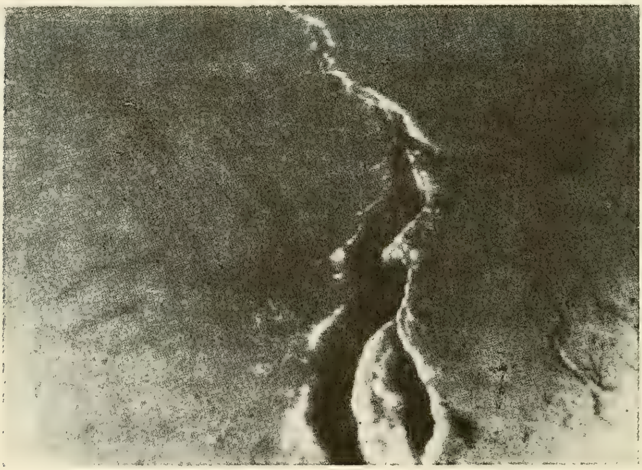


Fig. 39. Track of sika deer in Mordov preserve. March, 1954. Photograph by G.I. Il'ina.

In the Far East, when farm deer are fed hay and twigs in winter and spring, about 1.0 to 1.5 hectares of pasture is adequate per animal, but in this process the vegetation of the area allotted is gradually depleted.[54] If the vegetation is to be maintained in good condition, each deer should be allotted 10 to 15 hectares of pasture. Such an allotment is uneconomical, however, as this ratio would greatly enlarge the farm area required (Mirolyubov and Ryashchenko, 1948).

Daily activity and behavior. In summer in Primor'e region sika deer feed mainly in the morning and evening; the winter rhythm of feeding is not so well regulated. The mobility of deer is greatly hindered during snowfall and the animals stay bedded down; on clear days, during frosts, their activity notably increases. In winter, when winds are gusty, the animals look for shelters in sections of dense forest and bed down in becalmed places. In preserves in the European part of the USSR the daily rhythm of sika deer has yet to be fully ascertained.

The weight load carried by sika deer per sq cm area of hooves is 830 to 1,140 g, or an average of 960 g (Bromlei, 1956), which is significantly greater than the corresponding values for other ungulates of the Soviet Union. The heavy load on the hoof of the animal and its relatively small structure makes it very difficult for it to reach food and move about on thick snow. At a snow cover of 60 to 65 cm thickness deer progress only by hops and soon exhaust themselves. In the absence of snow they are capable of running swiftly for quite some time and easily clear hurdles up to 1.7 m high (Bromlei, 1956).

Deer swim well. Instances are known of deer swimming 10 to 12 km in the sea, for example from Putyatinsk to Askol'd Islands (Abramov, 1954). In Oka preserve sika deer stand in water to protect themselves from blood-sucking flies (Il'ina, 1956).

115 The organs of hearing, vision, and smell are well developed in sika deer.

After rut adult males isolate themselves and live in winter in small groups. Herds of females include young deer of both sexes not older than two years. The gregarious tendency is generally more prominent in winter, especially in years of abundant acorn crops (Abramov, 1954). In Oka and Khoper preserves herds of up to 23 to 25 animals have been recorded in winter (Il'ina, 1955).

---

[54] When deer density is even higher, vegetation is rapidly exhausted. Under conditions of unsystematic grazing and a deer density of one animal per 0.5 hectare, up to 80% twigs and 25 to 50% herbaceous vegetation of the park were depleted in one year's time (Ryabova and Saverkin, 1937).

Seasonal migrations and transgressions. Nearly the entire population of sika deer in Primor'e region winters on the eastern slopes of Sikhote-Alin. Commencing from December deer congregate on the southern and southeastern parts of the slopes and most move closer to the sea by descending into the broad-leaved forest belt. Most of the animals are confined to open valley regions, well-protected from cold westerly mountain winds blowing down the slopes (Bromlei, 1956). At the end of the 1940's on the large western slope of Sikhote-Alin there was only one small wintering site; in Sikhote-Alin sanctuary animals live along the steep parts southward (V.D. Shamykin).

In Primor'e region where heavy snowfalls are not rare in February and March, deer are compelled to migrate even closer to the sea. In this period most remain within 3 km of the sea; the population is scattered into several isolated groups living on relatively steep and less snowy (up to 30 cm) slopes. When the snowfall is particularly heavy, deer find refuge alongside tiny unfrozen streams and in littoral zones (Bromlei, 1956; and others). In winters of moderate intensity, even a minor snowfall can cause the movement of deer into less snowy sections of the region. After a few days the animals again scatter widely (G.F. Bromlei). In Sikhote-Alin preserve sika deer represent a more settled species compared to elk [moose] and Manchurian wapiti (V.D. Shamykin).

In May deer move into summer habitats, often selecting forest sections with dense undercover. When blood-sucking flies and ticks are numerous, some deer remain close to the sea coast and emerge into open, windy regions (Bromlei, 1956; and others).

In the European part of the USSR sika deer are characterized by seasonal migrations.[55] Such migrations are best seen in Khoper preserve; during the spring floods much of the Khoper becomes waterlogged and some deer move into the adjacent Borisogleb forest zone.

Reproduction. In Sudzukhin preserve rut commences between September 29 and October 11, but in 1944 a bellowing bull was heard on September 10;[56] the period of mass and most intense bellowing extends from October 7 to 23, lasting in various years for four to seven days. Rut ceases by November 5 to 8, more rarely at the end of October. The period of rut on the whole continues for 25 to 35 days but each adult female responds for less than a week. During the years when acorns are available rutting is very energetic. In October adult males move with small (three to four animals) harems of females. Compared to Manchurian wapiti, rut in sika deer proceeds more gently and no combats have been observed between males.[57] In the morning and evening adult males emit a whistling sound which ends in a hoarse howl. Usually the howl issues from those areas where deer have stamped out small (4 m^2) mating sites with their hooves. A single male usually makes six or seven such sites. In the period of rut males eat little and lose 20 to 25% of their normal weight (Bromlei, 1956).

---

[55] Il'ina (1956), without proof, contests this fact.

[56] In his conclusions Bromlei (1956) erroneously states (p. 213) that rut commences September 10 even though he has given correct dates earlier in the text (pp. 183 and 184).

Deer, at least females, may become sexually mature from 1.5 years, but most females do so in their third, rarely second year. Males
116 enter rut not before the third or fourth autumn of life; males 1.5 years of age do not bellow (Bromlei, 1956; and others).

Among acclimatized deer the period of intensive rut roughly coincides with that in Primor'e region, but on the whole is more prolonged. In Il'men preserve rut occurs from the end of September to the end of October (climax in mid-October); some individual males bellow even in early December. Usually rut is interrupted by snowfall and cold (P.M. Reshetnikov). In Khoper preserve, based on observations covering a period of 18 years, rut commences from September 18 to October 20, the very last bellowing males being heard on December 15. In an overwhelming majority of deer rut occurs in October and extends for an average of 34 days (D'yakov and Aleinikov, 1956). In some preserves bellowing males are heard even in January. In Moscow region most captive deer enter rut from mid-October to mid-November (Matyushin, 1954) and in Teberdin preserve from October 5 to 10 through mid-November (Kurapova and Stepanov, 1940).

The normal duration of gestation of sika deer is around 7.5 months; often it is a few days less (Mirolyubov and Ryashchenko, 1948; Matyushin, 1954). In Primor'e region barren females are encountered very rarely among wild deer. In Sudzukhin preserve the earliest case of normal fawning is seen between April 20 and 30 and the last on June 18; most fawning occurs mid-May. A female with more than one fawn has never been encountered but once two embryos were found in a dead female on dissection (Bromlei, 1956).

In most acclimatized deer fawning occurs in June; some individual females may fawn in July-August or even in September-

---

[57] In preserves in the European part of the USSR where the sex ratio is evidently different, intense combats are common between males; in Khoper preserve instances of male deaths in the course of combat have been recorded (D'yakov and Aleinikov, 1956). Intense combats between males are also common in farms where deer are raised for their velvet antlers.

November. Three instances of twins, all in Il'men preserve, were observed over a period of 16 years, starting from the commencement of acclimatization (Arsen'ev, 1949; Il'ina, 1956).

In velvet antler husbandry rut and fawning of sika deer occur at a much later period than in wild deer in the Far East and, generally, less evenly; some females become sexually active only in early winter. A single male mating with 5 females is considered normal; strong bulls can mate with 10 to 20 females. Barrenness is considerably more than in wild forms and, in some farms, as high as 30 or even 70%. Usually, there is a single fawn; twins are rare. Some females, commencing from the age of 1.5 years, fawn annually.

Growth, development, and molt. Newborn deer remain helpless for the first few days, lying down most of the time; mothers graze in the vicinity. Most fawns suckle for four to five months. In Sudzukhin preserve a lactating female was observed in November and one was once caught in January. Ten to 20 days after birth the young commence grazing independently. They remain with the mother until the spring of the following year, however, and sometimes even longer (Bromlei, 1956; and others).

Newborn bucks of captive animals weigh 4.75 to 7.32 kg (12 observations) and does 4.2 to 6.2 kg (9 observations). By age 9 to 12 months wild male fawns weigh 49 to 59 kg and female fawns 48 to 55 kg; at the end of 16 months weight is 70 to 75 and 65 to 70 kg respectively; in winter fawns gain almost no weight. After two years weight increase slows down. Around that age males start outstripping females noticeably in growth. The maximum weight of males is recorded at 7 to 10 years and of females at 4 to 6 years. In Sudzukhin preserve the maximum, correctly established, weight of a male was 131 kg and that of a female 85.7 kg; corresponding weights in velvet antler farms were 148 and 112 kg respectively (Mirolyubov and Ryashchenko, 1948; Matyushin, 1954; Bromlei, 1956).

At age 1.0 to 1.5 years milk incisors are replaced by permanent ones and at age 2.0 milk molars also replaced. By the tenth month small "tuberosities" (3.5 cm) are visible in males at the place of future antlers; by April the first tiny unbranched antlers have begun to grow. "Shilniks" bear such antlers around the first year of life (up to May–June of the following year). As soon as these are shed branched antlers, or the first velvet antlers, begin to grow. In nurseries the maximum growth of antlers is achieved at the age of 10
117 to 12 years. In Primor'e region adult deer shed antlers at the end of April or in May; at the end of May–June young velvet antlers begin to appear. In September deer rub the velvet off their antlers (Bromlei, 1956). With a month's delay, or more rarely around the same

time as in Primor'e, the shedding of old and the growth of new antlers take place in deer in preserves of the European part of the USSR, in the Caucasus, and in Trans-Urals (Kurapova and Stepanov, 1940; Il'ina, 1956).

The juvenile spotted coat is discarded after the autumn molt. In the Primor'e region spring molt of adults commences in the first 10 days of March (hair of the beard falls first), peaks in the latter half of April to early May, and ceases in the last 10 days of May. In the sick and ailing molt is delayed. The summer coat is sparse, shorter than the winter one, and almost devoid of underfur. Winter hair begins to grow perceptibly at the end of August and by mid-September, or slightly earlier, deer acquire their winter coat and hair growth is negligible thereafter (Bromlei, 1956; and others). In preserves of the European part of the USSR spring molt of deer occurs after a slight delay compared with the Far East; moreover, it is more extended in the above preserve (Il'ina, 1956).

According to observations made in velvet antler farms the maximum life span of sika deer is 18 to 21 years; females older than 15 years can still breed. In nature deer older than 11 to 14 years usually do not survive as they are killed by predators or die from other causes (Mirolyubov and Ryashchenko, 1948; Bromlei, 1956; and others).

Enemies, diseases, parasites, mortality, competitors, and population dynamics. Among various factors causing death of sika deer, predators, especially gray wolf, are of maximum importance. In Mordov preserve from 1948 to 1952 the death of 111 sika was recorded, of which 50 (45%) were caused mainly by wolves and partly by lynxes, 25 were due to emaciation and disease, 4 to traumatic injuries, etc. (F.D. Shaposhnikov). In Oka preserve 27 instances of deer mortality were reported from 1938 to 1951, of which 12 (44%) were caused by wolves, 6 by dogs, 1 by lynxes, 3 by disease, and 4 by drowning in floodwaters flowing under ice (Kozlov, 1954). In Khoper preserve from 1939 to 1947 no less than 50 deer were destroyed by wolves, of which 11 were killed in 1943 alone (Arsen'ev, 1949; and others). During the 17 years of acclimatization in preserves of the European part of the USSR, the Caucasus, and Trans-Urals, 383 instances of death of sika deer have been registered; of these, 45.7% were caused by wolves, 0.5% by lynxes, and 3.1% by stray dogs (Il'ina, 1956).

In Sudzukhin preserve 5 to 30% of the population of sika deer are killed annually by wolves (gray). In the feces of wolves (gray; 59 samples) the remains of sika deer were detected in 16.9% in January and February, 39% in March, 22.2% in April, and in much smaller numbers at other times. Thus wolves cause maximum damage to sika deer of Sudzukhin preserve in the second half of winter when the snow cover is usually maximum and frozen snow crust forms often. This is also the time of massive ice formation on rivers and deer slip on ice helplessly (Bromlei, 1956). In attempting to save themselves from wolves deer of Sudzukhin preserve often run into dense shrubs, penetrate relatively deeply into rivers, or find refuge in the sea, where they remain sometimes for 30 to 40 minutes and swim 400 to 1,000 m or even farther away from the coast. On frosty, slushy days many lose their stamina, their lungs become inflamed, and death ensues; pregnant females often abort (Bromlei, 1956). In Kedrovaya Pad' preserve 83 deaths of sika deer were recorded from 1926 to 1936; deaths were due mainly to red and partly to gray wolves (Mirolyubov and Ryashchenko, 1948). In Khoper preserve several deer have been killed by wolves in the least snowy winters, when the lakes are not fully covered with ice and deer slip and often fall into them (D'yakov and Aleinikov, 1956).

Apart from the predators mentioned above, sika deer are also threatened by Far East leopards and tigers, but their numbers are insignificant. Fawns, especially up the age of two months, are threatened by bear, Far East leopard cat, red, fox, and yellow-throated marten. Instances of attack by predatory birds are not known. Sudzukhin preserve has registered six deaths of deer caused by stray dogs 118
(Bromlei, 1956; and others).

Sika are susceptible to foot-and-mouth disease, rabies, carbuncular emphysema, necrobacillosis, hemorrhagic septicemia (pasteurel-

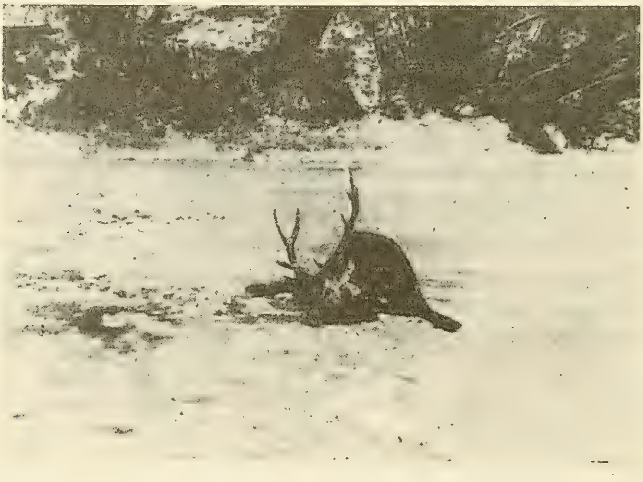


Fig. 40. Male sika deer dead on slippery river ice. Khoper preserve. October 1954. Photograph by G.I. Il'ina.

losis), Siberian uclers, tuberculosis, leptospirosis, actinomycosis, ringworm, and coccidiosis. From 1932 to 1940 in the velvet antler farms of Primor'e region 470 deer died of necrobacillosis and 134 from hemorrhagic septicemia (Mirolyubov and Ryashchenko, 1948; Vysotskii and Red'kina, 1954; and others). Instances of deer mortality due to hemorrhagic septicemia have also been reported from Oka and Teberdin preserves and as a result of foot-and-mouth disease from Buzuluk Bor (Il'ina, 1956).

In Primor'e region and in places of acclimatization only a few species of helminths have been detected in wild sika. In Sudzukhin preserve 75% of adult deer were once infected with the liver fluke *Dicrocelium lanceolatum* (Bromlei, 1956). Among animals held in feedlots 4 species of trematodes, 3 species of cestodes, and 29 species of nematodes have been recorded (Abramov, 1954). Between 200 and 500 ticks (*Dermacentor, Ixodes,* and others) were found in early June in some wild sika deer. Deer also suffer from gnats (mainly *Simulum maculatum*), biting midges, horseflies, sucking lice (*Lipoptena cervi*), body lice, and other ectoparasites. Severe parasitism by nasopharyngeal gadfly has been established in deer in feedlots but wild deer are not invaded by it (Bromlei, 1956).

In snowy and severe winters in Primor'e region (1877–1878, 1914–1915, 1928–1929, 1934–1935, 1938–1939, 1941–1942, and 1947–1948) a considerable number of deaths of deer due to emaciation, predators, and poachers were registered. The winter of 1947–1948 was particularly damaging when, in Sudzukhin preserve, up to 50% of all the deer died; in some adjacent regions mortality was 100%. When the snow cover (over 40 cm on relatively steep slopes) does not remain longer than a month, deer can withstand such winters relatively well (Bromlei, 1956).

Roe deer and Manchurian wapiti occupy the same habitats as sika; however, in view of the relatively low population of ungulates in the regions of their coexistence in the Far East, competition between these species is negligible. In Il'men preserve, of the 125 plant species which are satisfactorily and well consumed by sika deer, roe deer consume about 90 (Averin and Ushkov, 1947).

Captive sika deer can interbreed with other deer (maral, Manchurian wapiti, and Crimean red deer); in nature, such instances are extremely rare.

119 The population pattern of wild sika deer in Primor'e region can be judged from the following data: of the 38 deer which died in Sudzukhin preserve, 55% were not older than two years and only 5% older than 10 years (Bromlei, 1956). Two instances are known when 15 sika protected from wolves grew to a herd of 2,000 to 2,500 ani-

mals in 30 years (Sidima Peninsula and Askol'd Islands). In Oka preserve the annual herd growth averaged 20% (Kozlov, 1954) and in Khoper 14.6 and 31.1% from 1938 to 1953 and 1954 respectively (D'yakov and Aleinikov, 1956). In Askaniya-Nova 80 to 93% of newborns survive up to six months (Salganskii, 1952).

Among embryos and newborn animals males occur about 1.5 times more often than females. After a few months this ratio changes in favor of females because of high male mortality. In 1945 in Sudzukhin preserve 216 females and 54 males of sika deer were counted; thus, the sex ratio was 4:1 in favor of females (Bromlei, 1956). In Oka preserve the ratio of male to female is 1:3 (Il'ina, 1956).

Field characteristics. In growth sika deer lag noticeably behind red deer *Curvus elaphus,* especially Manchurian wapiti. Only some individual large male sika deer attain a height of 120 cm at the withers, while even female Manchurian wapiti reach 118 to 135 cm, on the average 128 cm, at the withers. The summer coat is characterized by distinct spots. In size of hoofprints and feces sika deer fall between Manchurian wapiti and roe deer (Formozov, 1952). The pace is 45 to 65 cm, which on trotting lengthens up to 75 to 110 cm, when jumping up to 3 to 3.6 m, and when jumping over ravines up to 6 m. Sika strip the bark of trees in narrow longitudinal bands and not continuously as done by Manchurian wapiti; they do not remain for long near a single tree (Bromlei, 1956). Before lying down sika rake up the snow (if it is wet) or lie directly on it (when the snow is high and dry). Stamped tracks are characteristic of sika deer.

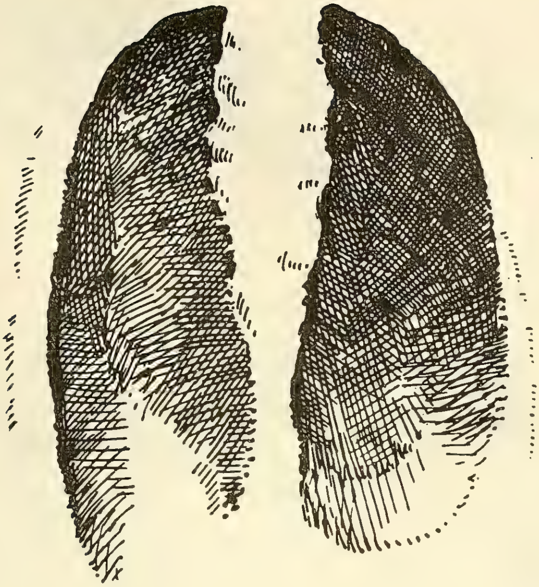
Females emit a loud whistling call which terminates in a hoarse rattle. Young males also whistle in a similar manner, but without the rattle at the end. Adult males usually call only during rut (Bromlei, 1956).

The summer fur of adult males and females is similar; the main shade is rust with white spots (in females the color is somewhat lighter). In winter differences are more distinct: in females the general background is light gray, and in males, olive-brown and generally even darker. (A.N.)

Economic Importance

120 In view of the low population of wild sika deer their hunting has long been prohibited. In the nineteenth century most deer were caught on rocky littoral shoals or islets in long enclosures in which pits were dug. Russian game hunters used to chase the deer toward the sea and then shoot them.

The meat of this deer is good; the quality of male meat is at its



119 Fig. 41. Hoofprint of male sika deer (magnified). Primor'e region. June, 1928 (from Formozov, 1952).

best in September, i.e., before rut, and the female meat in September to November. Hides can be used to make chamois, rugs, and various articles. Young unossified velvet antlers[58] are considered the most valuable deer product; from these antlers is prepared the powerful tonic, pantocrine. The curative properties of velvet antlers of sika are rated superior to those of other deer and hybrid forms. Studies conducted on a small amount of material in Mordov preserve revealed that the velvet antlers of deer acclimatized there possessed only little "activity" (Arsen'ev, 1949). This conclusion is of utmost importance; without testing, it cannot be applied to other regions of deer acclimatization. The largest and best velvet antlers are found on deer 7 to 8 and 11 and 12 years of age.

The great demand for velvet antlers and their high value in the Chinese market promoted development in the Soviet Union of a special branch of animal husbandry—raising sika deer to obtain velvet antlers. In the Far East the confinement of deer in paddocks was instituted at the end of the 1880's. Such small individual farms

---

[58] Velvet antlers of stage V, before the commencement of ossification of the cartilaginous mass, are valued most. In wild deer of Sudzukhin preserve this stage corresponds to the period June 15 to 20 (Bromlei, 1956).

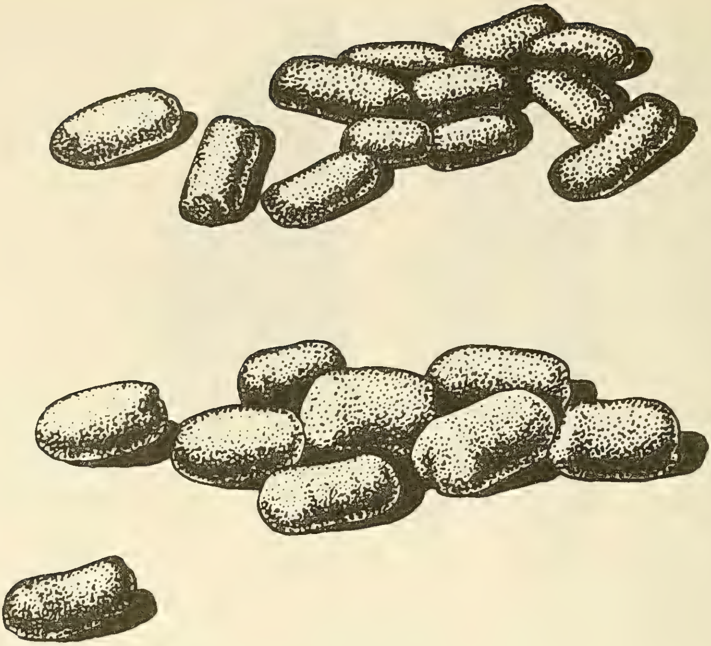


Fig. 42. Winter feces of female (top) and male (bottom) sika deer (natural size). Sudzukhin preserve. Sketch by G.F. Bromlei.

have greatly multiplied in present-day Khasansk, Suchansk, and Shkotov regions, and in southern Ol'ginsk and Terneisk regions. 121 Large parks also existed, for example, Yankov park on the Sidima Peninsula (Abramov, 1954). In 1928 deer farms and parks were nationalized and formed the basis for large state farms in which deer were raised to obtain velvet antlers. In the mid-1930's over 8,500 sika deer were held in Primor'e state farms and 1,000 in collective farms (Ryabova and Saverkin, 1937). Sika were imported into nurseries of the Irkutsk region and the Altai (initially in 1933 into Shebalino, and later into Kaitanak, Nizhnii Uimonsk, and the upper courses of the Katun) and held in common paddocks with maral or separately. In the mid-1950's there were up to 20,000 sika in such nurseries (Il'ina, 1956).

As a result of diminished demand for velvet antlers in the international market future prospects for velvet antler farming are not clear. Neither are the prospects clear for such products as three- to four-month-old embryos removed from the womb of female deer, tails, penises, etc., which have a market in China. The importance of other marketable products of sika (sinews, ossified horns, and leg bones) is relatively insignificant.

In the past, when these deer were far more numerous, they threatened plantations in some remote forest segments. At present, however, they must be strictly conserved everywhere. It is also extremely desirable to reacclimatize sika deer in regions of Primor'e where they existed in the past but were subsequently exterminated. It is also possible to release these deer on some islands near Vladivostok. (A.N.)

4. TRUE, WELLBORN [RED] DEER

Cervus (Cervus) elaphus Linnaeus 1758[59]

1758. *Cervus elaphus.* Linnaeus. *Systema Naturae,* 10th ed., vol. 1, p. 67. Southern Sweden.
1777. *Cervus elaphus hippelaphus.* Erxleben. *Syst. Regni Anim.,* vol. 1, *Mammalia,* p. 304. Ardennes.
1777. *Cervus elaphus canadensis.* Erxleben. *Syst. Regni Anim.,* vol 1, *Mammalia,* p. 305. Eastern Canada.
1840. *Cervus maral.* Ogilby. *Rep. Council Zool.,* p. 22. Nomen nudum.
1841. *Cervus affinis.* Hodgson. *Journ. Asiat. Soc. Beng.,* vol. 10, pt. 2, p. 721. Chumbi valley in Sikkim.
1850. *Cervus maral.* Gray. *Knowsly Menagerie,* pls. 38 and 39. Caspian province of Iran.
1867. *Cervus xanthopygos.* Milne-Edwards. *Ann. Sc. Nat. Zool.,* vol. 8, p. 376. Peking environs (possibly northern Manchuria, Ussuri).

[59] Usually the European form called the red deer is considered a separate species, distinct from izyubr, maral, American wapiti, Bukhara deer, and other forms, which are also often treated as separate species. After it was demonstrated that all these forms shared a common species background (Heptner, 1940; Heptner and Tsalkin, 1947), and this viewpoint became generally acknowledged, it became more advantageous to combine these species under the Russian name "true deer," which is distinct from spotted and other deer. The popular names "maral," "Manchurian wapiti," etc. are, of course, best retained for some individual varieties or groups of varieties. It is meaningless to call the Russian maral by the American name wapiti, as is sometimes done.

Both these names are artificial and bookish. The Russian popular name of this species in the western part of the geographic range, in the Caucasus, and in Central Asia is "deer," in Siberia "maral," and in Trans-Baikal and the Far East "izyubr". Among hunters the adult male is called a bull, the adult female "olenukha" or "maralukha," and a two-year-old deer with simple antlers "saek" or "spichak".

1872. (1873).[60] *Cervus maral* var. *songarica*. Severtsov. *Vertical and Horizontal Distribution of Turkestan Animals*, p. 109. Eastern part of Trans-Iliisk Alatau (upper course of Turgena).[61]

122 1872. (1873). *Cervus maral* var. *sibirica*. Severtsov. *Vertical and Horizontal Distribution of Turkestan Animals*, p. 109. Type locality has not been directly indicated but it is clear from the text that the Altai should be regarded as such. The region of Lake Telets (Altai preserve) is suggested as *terra typica restricta*. Nec *Cervus sibiricus* Schreber, 1784.

1874. *Cervus caspicus*. Brook. *P.Z.S.L.*, p. 407. Locations southwest of Caspian Sea.

1876. *Cervus eustephanus*. Blandford. *P.Z.S.L.*, 1875, p. 637. Tien Shan in China.

1880. *Cervus lühdorfii*. Bolau. *Abh. Naturw. Hamburg.*, vol. 7, p. 33. Northern Manchuria, "Buryatskaya steppe".

1886. *Cervus caspius*. Radde. *Fauna u. Flora d. südwestl. Caspi-Gebietes*, p. 10. Talysh.

1889. *Cervus isubra*. Noack. *Humboldt*, vol. 8, p. 12, fig. 8. Names based on the same specimen used for *lühdorfii*.

1892. *Elaphus ussuricus*. Heude. *Mém. Hist. Nat. Emp. Chin.*, vol. 2, p. 113. Ussuri.

1897. *Cervus bedfordianus*. Lydekker. *P.Z.S.L.*, 1896, p. 932. Manchuria.

1898. *Cervus canadensis asiaticus*. Lydekker. *Deer of All Lands*, p. 104. Region south of Lake Telets near Yenisy source, i.e., the present Altai preserve.

1900. *Cervus bactrianus*. Lydekker. *Ann. Mag. Nat. Hist.*, vol. 5, p. 196. Russian Turkestan, probably Bukhara. Also suggested are the upper courses of the Amu-Darya and its tributaries in Tadzhikistan.

1902 *Cervus wachei*. Noack. *Zool. Anz.*, vol. 25, p. 146. Chingil'ta, valley, near Chernyi Irtysh, Kobdo.

1903. *Cervus vulgaris*. Botezat. *Morph. Jahrb.*, vol. 32, p. 154. New name for *elaphus*.

1903. *Cervus vulgaris campestris*. Botezat. *Morph. Jahrb.*, vol. 32, p. 154. Carpathians, Bukovina (lower belt of mountains).

[60] On the title page, 1873; released at the end of 1872.

[61] N.A. Severtsov (1872–1873) states that his material for the description of Tien Shan forms was two adult males and one young deer caught "at the end of October in Trans-Iliisk Alatau, east of Vernii [Alma-ata], on the peak of Turgena and at Santash Pass near the eastern end of Issyk-Kul' " (p. 103). There is no justification for considering "Dzhungarsk Tien Shan and probably Kuldja" a type locality (Lydekker, 1915; Ellerman and Morrison-Scott, 1951).

1903. *Cervus vulgaris montanus.* Botezat. *Morph. Jahrb.*, vol. 32, p. 155. Carpathians.
1904. *Cervus hagenbecki,* Shitkov. *Zool. Jahrb. Syst.*, vol. 20, fig. 4, p. 103. Turkestan.
1907. *Cervus balticus.* Matschie. *Weidwerk in Wort und Bild.*, vol. 16, p. 186. Polish Baltic. Libemyul'.
1907. *Cervus biedermanni.* Matschie. *Sitzungsber. Ges. Naturf. Freunde, Berlin,* p. 223. Telets, Altai.
1914. *Cervus caucasicus.* Winans. *Amer. Mus. Journ. Zool.*, vol. 14, p. 67. Nomen nudum.
1915. *Cervus canadensis baicalensis.* Lydekker. *Cat. Ung. Mamm. Brit. Mus.*, vol. 4, p. 134. Sayan and Baikal mountains west of Lake Baikal. Given as substitute for *Cervus maral* var. *sibirica* Severtsov,* 1872.
1920. *Cervus elaphus brauneri.* Charlemagne. *Animals of the Ukraine.* Forests of hilly Crimea. (Formal description not available. Only a new name with a reference to the description in Brauner's work, 1900 is given).
1925. *Cervus elafus* (Sic!) *tauricus.* Fortunatov. *Sbornik Askaniya-Nova,* p. 324. (name) and p. 326 (description). Crimea and Crimean preserve (forest near Koz'modem'yansk monastery).[62]
1956. *Cervus elaphus carpathicus.* Tatarinov. *Animals of Trans-Khidnikh Region of the Ukraine,* p. 103. Eastern (Soviet) Carpathians.[63] (V.H.)

Diagnosis

Summer coat of adult animals has no spots (a small number of spots on the back, sometimes also on the sides, are present as an exception in some forms in females, more rarely in males); the first coat of fawns is spotted. Speculum large and rises above the croup on the base of the tail. Antlers usually have not less than five tines (with an ice [bez] tine above the eye besides), which form a crown in some individuals. Tail at relatively short; length less than that of ear. Height at withers of adult males exceeds 115 cm. (V.H.)

---

*Spelling of author's name in taxonomic divisions is sometimes at variance with spelling in text and bibliography since the Israeli orthography has been followed in this translation.

[62] It is possible that this name has an advantage over *brauneri* since the latter has not been assigned fully in accordance with the rules of nomenclature.

[63] This name is a synonym for the forms *campestris* and *montanus.* Since their descriptions are not completely satisfactory, the name given by K.A. Tatarinov could have been of importance to nomenclature but the description has been given without conforming to the rules of nomenclature and thus it is essentially a nomen nudum.

Description

Large deer; largest species of the genus and the second largest in the family. Build slender and proportionate but in general somewhat heavier than that of spotted deer. Neck relatively short; head of adults fairly raised but relatively lower in fawns. Ears moderate in length, proportionate, directed forward, coming up to the eyes and shielding them (length about one-half length of head). Tail short, roughly about one-half length of ear.

Antlers of red deer when fully developed usually with not less than five tines (two brow, one central, and two terminal). Presence of bez tine, which in deer inhabiting the Soviet Union is absent only as an exception, is a characteristic feature of the species. In other features antlers highly variable, both individually and geographically. In several races an increase in number of tines up to 20 occurs in extreme cases and even more in some exceptional cases. Individual and geographic variability are seen not only in number of tines but also in degree of development (size, mass, and weight) of antlers, relative size of tines, their position in relation to each other, form of beam, and placement of antlers, i.e., degree of proximity of beam and position in relation to the sagittal body plane. Antlers may be fairly vertical and close-set or turned sideways. Individual variability in structure of antlers is fairly high, but each race has a characteristically predominant antler type. Moreover, the range of variability of antlers in individual subspecies is fairly definite: in some it is slight, in others considerable, and in still others maximal.

In general there are three main types of antlers[64]: 1) *Central European (hippelaphoid or elaphoid) type.* Number of tines large, primarily because of branching of antler tips into so-called "flare"; tines set like tufts in different planes. Brow, bez, and central tine form normally; bases of first two usually close and first or third tine best developed. European deer sport such antlers, in which the number of tips can be particularly high; this type is also seen on Caucasian deer. Also encountered in the Caucasus are antlers of a more simple structure, with about five tips not in the form of a crown. Thus individual variability is maximum in this type.

2) *Maral type.* Antlers larger and can attain extraordinary proportions. Beam usually thick, with six or seven or more tines in exceptional cases. Crowns do not form and terminal tines set in a

---

[64] For more details, see Heptner and Tsalkin (1947).

single plane (sagittal or close to it). Fourth tine largest in size. Brow, bez, central tines well developed; distance between the first two fairly 125 large. Usually, at the point of deviation of the fourth branch, beam bent backward (downward), sometimes very sharply. Antlers generally well spread out. This type is characteristic of maral of Tien Shan and Siberia and Manchurian wapiti of Siberia and the Far East.

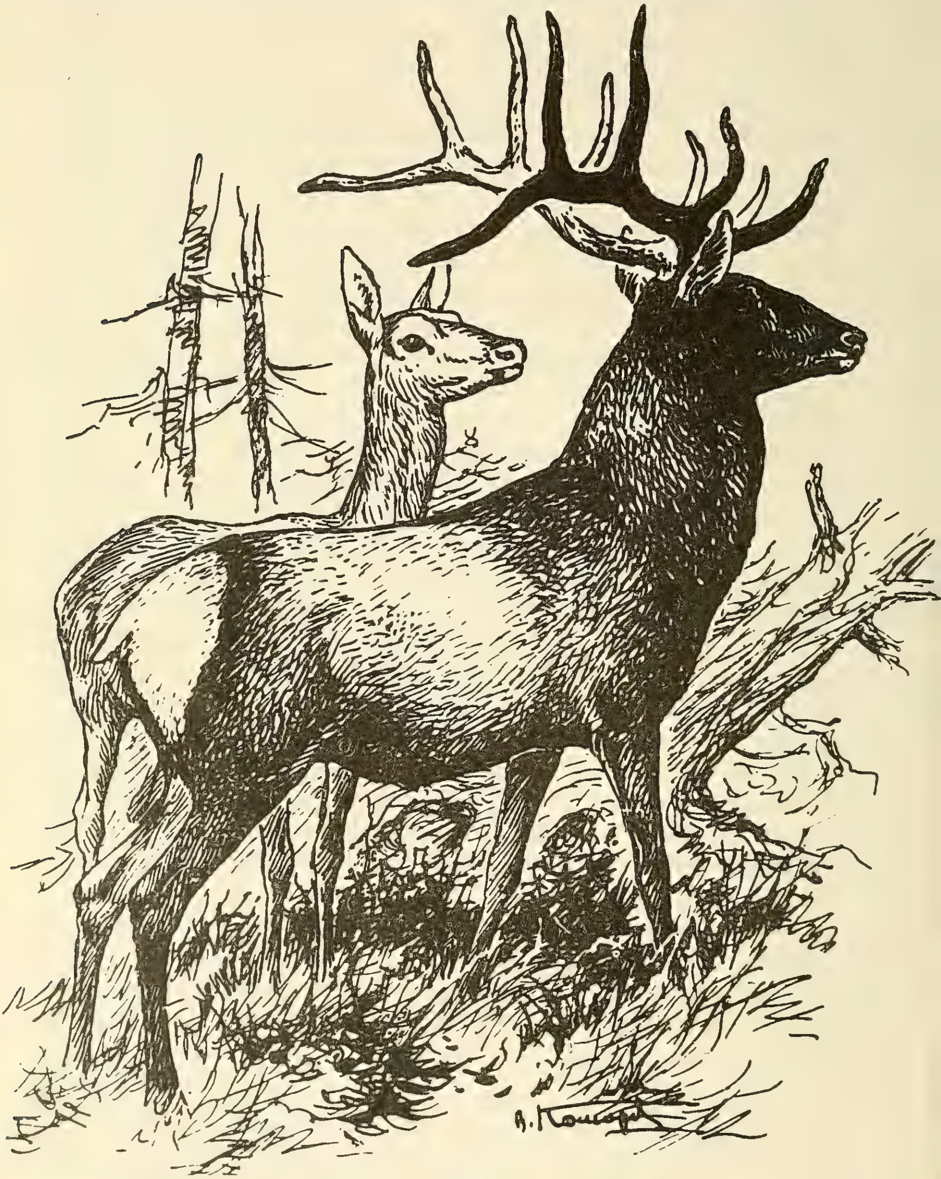
3) *Hangul* (*Central Asiatic*) *type.* Simplest of antler types. Antlers relatively small although quite massive and usually with no more than five tines (brow, bez, central, and two terminal which form a fork). Sometimes a sixth tine occurs but there is no true crown. Fork often so set that its plane forms a large angle, sometimes almost perpendicular, to the sagittal plane of the body. Bez tine often relatively high and quite separated from the brow tine; often, central tine also set high. Position of the antlers differs but usually they are set fairly perpendicular. Deviations are relatively few. This type is characteristic of several Central Asiatic forms, e.g., Bukhara deer of Middle Asia among Russian forms.

The color of red deer is characterized by the absence of spots in all coats except the first. Yet in some geographic races spots are sometimes seen in the summer coat, more often in females than males, as an individual variation. When the spots are faint, two rows occur along the sides, running along the spine; when the spots are more intense, a large number are disposed along the back and sides. The frequency of this variation differs in different geographic races. Among Russian forms spots are seen in Bukhara deer (*C. e. bactrianus*) but most often in Caucasian deer (*C. e. maral*). In other races they are imperceptible or extremely rare.[65] Individual coloration, primarily overall shade and intensity, is characteristic of all races. Thus light rusty and dark brownish-gray are seen among maral as extremes, together with all intermediate combinations of these shades. Intensity of color of individual body parts and the contrast between fairly intensely colored parts, etc., also vary considerably.

Coloration of deer undergoes intense geographic variability. As a typical example the color of Altai maral (*C. e. sibiricus* Sev.) is described here; the specific characteristics of individual races are discussed below under the section "Geographic Variability". Hair color of males on the back and sides is light and grayish-brownish-yellow, varying intensely depending on the predominance of one or the other shade. Speculum large, broad, and spreads onto croup: coloration of speculum in individual animals varies from dull rust

---

[65] Among forms living outside the Soviet Union spots are particularly frequently manifest among Corsican deer (*C. e. corsicanus*) and evidently also among Atlas deer (*C. e. barbarus*). According to some data spots are fairly distinct in most Corsican deer in summer. It is, however, incorrect to assume that the summer as well as winter coat is invariably spotted in all adult animals of this form (Flerov, 1952).



124 Fig. 43. Maral (*Cervus elaphus sibiricus* Sev.). Sketch by Komarov.

to straw. At the top and from the sides it is rimmed by a dark band. The extent of the dark rim varies widely: sometimes it is noticeable only from the sides and in other instances also covers the speculum from above. The color of this band varies from dull brown to true cinnamon. On the neck and back, in the mid-dorsal region, a dark streak occurs, which is discernible all along the back, but sometimes disappears behind the shoulder blades. On the speculum the continuation of the streak running on the back is most often well developed in the form of a fairly bright dark brown band, but this is absent in some cases. Tail and speculum of the same color. Legs and abdomen dark cinnamon-brown, contrasting sharply with the color of the trunk. Mane of long, coarse, cinnamon-brown hair well developed on the neck. Head brown or cinnamon-brown but lower lip light in color (grayish- or brownish-rust). Rings of a much lighter color encircle the eyes.

The winter coat of females is more uniform in color, without the sharp contrasts characteristic of males. Main color of hair on back and sides grayish-brown and darker than that of males. No darkening of abdomen and limbs occurs. Abdomen and inner surface of legs lighter in color than sides and back. Limbs grayish or cinnamon-brown. Mane on neck much less developed but color similar to that of males. Dark streak on back and edge of speculum more pronounced than in males.

It should be pointed out that the color of areas such as the speculum, its rim, and the dark streak on the back are clearly seen toward the end of molt, becoming appreciably duller later. This is equally true of males and females.

The coloration of maral is more uniform in summer than in winter, and sex-related color dimorphism is very poor at this time. The general shade of body color is brown-cinnamon without darkening of neck, abdomen, and limbs. The cinnamon shade is somewhat more vivid in females than in males. The dark streak on the neck and back is also more distinct in females although it often disappears behind the shoulder blades. The speculum is rust-colored, or various shades of this color, but brighter than in the winter coat. A dark brown band, sometimes faint, traverses midline of the speculum. The dark rim is also brighter than in the winter coat.

Not only the general color tone but also the coloration of individual body parts undergo geographic variability. In different races seasonal coloration varies in individual animals and the contrast between winter and summer coloration is also variable. In European and Caucasian deer the contrast between the relatively bright rusty summer coloration and the dull grayish-brown winter coat is sharp; it is less marked in maral and Bukhara deer but again prominent in izyubr.

In the first coat of young maral the forehead and crown, upper part of the neck, and back and sides of the body are brown and relatively dull. The rest of the head, lower surface of the neck, and legs and abdomen are lighter in color than the sides and back, and the cinnamon color of these parts has an admixture of grayish-brown. Speculum large and rusty-red; upper surface of the tail also rusty-red. Speculum encircled by a fairly bright cinnamon-brown band. A dark brown streak runs along the neck and back, extends to the caudal base, and passes through the speculum where it turns into a cinnamon-brown color. Along the sides of the streak on the back and also partly in the region of the base of the neck two rows of distinct, well-defined, white spots occur. These white spots are scattered on the rest of the back, sides, in the region of the shoulder blades, and on most parts of the thighs, where they are also white in color but less sharply so and not as close-set. In time the spots become less distinct. With the commencement of autumn molt the spots gradually disappear and by winter the young animal sports an adult coat.

The coloration of young animals also shows marked individual variability, primarily in overall shade and number of spots. In related groups coloration of fawns does not differ but differences are quite prominent in distinct subspecies.

In general the intensity of coloration of the young evidently corresponds to that of adults (see section "Geographic Variation").

The skull structure, typical of the genus, stands out prominently due to its large size (differences from sika deer were discussed while describing that form).

The size of body and skull and the gross weight exhibit intense individual and geographic variability. Weight of the largest races of the species exceeds a few times that of the smallest. Furthermore weight varies greatly in different seasons. In the period of rut a stag may lose up to 20% of its initial weight. The animal attains full development by the age of four or five years and, at that time, stags of the largest Russian race, maral (*C. e. sibiricus*), measure as follows: 127 height at withers 150 to 155 cm, condylobasal length of skull up to 450 mm, and weight up to 300 kg. Females are significantly smaller and lighter than males.

Newborn maral measure 74 to 77 cm at the withers and 92 to 101 cm in body length. Their weight on the first two to six days averages

16 kg (Tsalkin, 1944).[66]

These deer sometimes give rise to hybrids with sika. Hybrid characteristics have been described in the section pertaining to sika deer. (V.H.)

Taxonomy

Cervus elaphus can be considered the most progressive species not only of the genus, but also of the entire subfamily Cervinae. The total loss of spots, an infantile feature, in adult animals can be considered an advanced characteristic. Far East sika deer (*C. nippon*) should evidently be considered the form nearest to *C. elaphus*. South Asian species are more isolated from it. Some are highly specialized. (V.H.)

Geographic Distribution

These deer are found in forest, forest-steppe, steppe, in part desert, and montane regions of the Old World, roughly between 25–30 and 55–60° N lat. and the very same topographic regions between 35 and 50–60° N lat. in North America.

Compared to its original state the geographic range of deer in the Old and New World has undergone extreme variations over the years. These changes concern general features as well as area, which has shrunk extensively. The primary factors affecting range size are extermination of the animal, particularly vulnerable because of its large size, and land cultivation, primarily in forest and forest-steppe regions falling in the temperate zone of the northern hemisphere, which represented the original range.

In some sections of the European part of the USSR these deer were exterminated so long ago (probably in the first millenium A.D. or possibly at its inception) that it is hardly possible today to reconstruct the former habitation of the animal with any degree of certitude.

Geographic Range in the Soviet Union (Reconstructed)

The boundary of the former range of deer in the European part of the USSR encompassed the Baltic region in the east at least up to Pskov, but probably more to the east, possibly even up to the southern coast of Lake Ladoga (encountered in the second half of the first millenium B.C. and in the ninth and tenth centuries A.D. at Pskov

---

[66] Some additional data are given in the section "Geographic Variability". For further details on morphology, taxonomy, and zoogeography, see Heptner and Tsalkin, 1947.

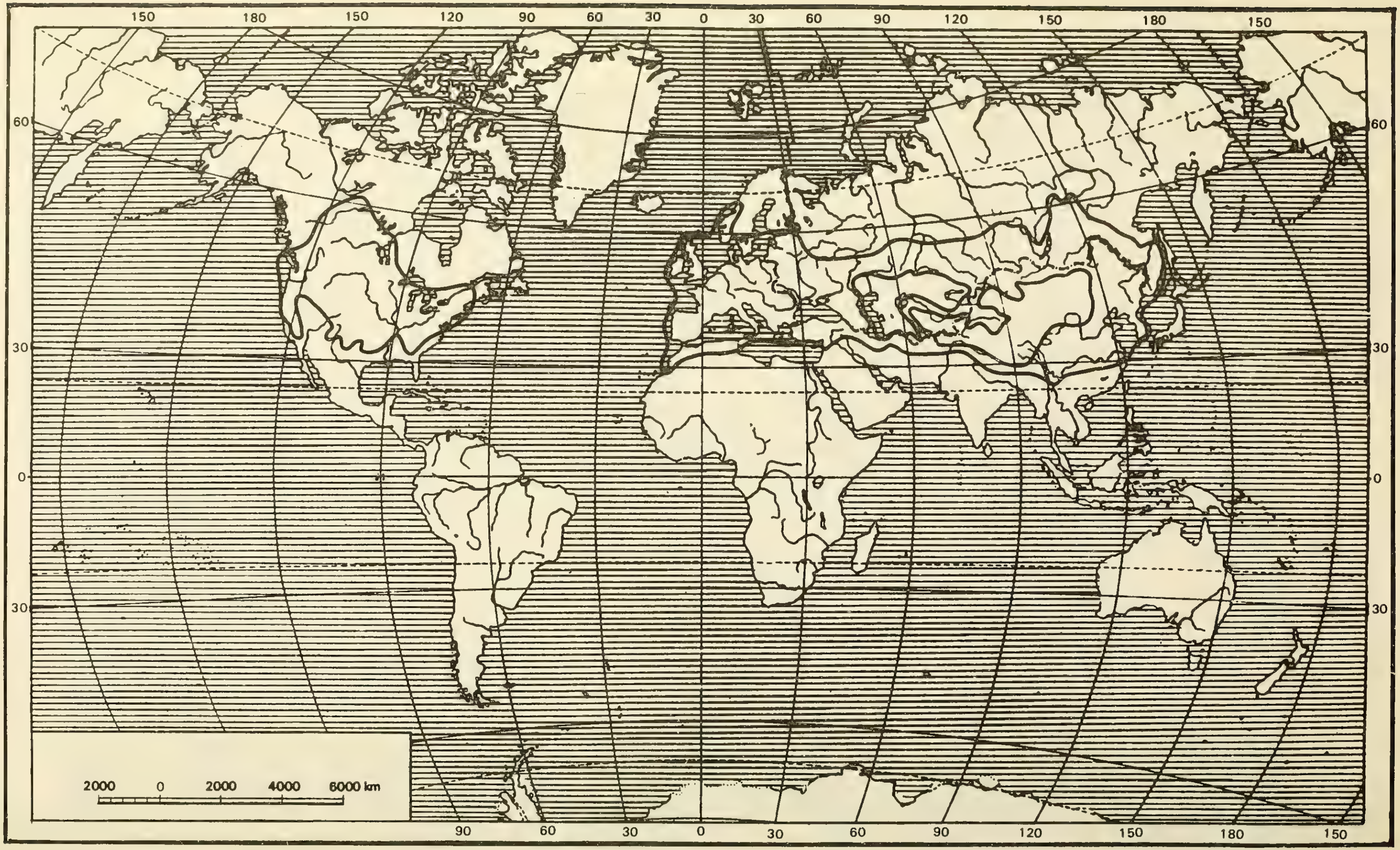

150
180
150
120
90
60
30
0
30
60
90
120
150
180
150
60
30
0
30
2000
0
2000
4000
6000 km
90
60
30
0
30
60
90
120
150
180
150

Fig. 44. Reconstructed species range of red deer (*Cervus elaphus* L.). Schematic (scale in km). V.G. Heptner.

and Old Ladoga). However, the animals were very rare. From the Baltic the boundary proceeded south, encompassing Belorussia and the western parts of the Smolensk region.

From there the boundary turned east, probably through the Kaluzh region (see below). The northern boundary of the range between the upper Dnieper and middle Volga is not accurately known. Deer undoubtedly lived throughout the Black Sea and Azov steppes, even in such places as Perekop, throughout the central Caucasian steppes, and also in the steppes around Stalingrad and along the Volga up to Astrakhan'.[67] In the north the occurrence of deer is known around Chuguev (close to Khar'kov) in the Belgorad region, in the Poltava region, in the regions of Mirgorod, Lubensk, Gadyacha, and farther north in Glukhov (east of Chernigov). Deer also lived in the Kursk region, Voronezh, and Morshensk (north of
129 Tambov). In the light of these data one may assume that deer evidently lived in the Trans-Oka forests (S.V. Kirikov), i.e., in Tul'sk and other places of the region south of Moscow. Somewhere south of the Oka, or along the Oka, the northern boundary of the range evidently proceeded into central Russia during the last 1,000 years or even last 500 years.

Deer also lived around Moscow but at a much earlier period (D'yakov culture—700 B.C. to 500 A.D.). At that time, however, they were rare (Formozov, 1947) and evidently exterminated long before Moscow was founded, since there are no records of this species. Deer which lived in the royal hunting grounds around Moscow (Ismailov menagerie, for example) were undoubtedly imported. Therefore, there is no adequate basis for considering Moscow an ancestral habitat of red deer (Flerov, 1952; map).[68]

Turkin's report (1900), with frequent references to F.K. Lorents, about the greatly isolated habitation of deer in the Nikol'sk basin district of Vologod, Galichsk-Kostrom, and Semenov-Nizhegorod, even in the 1880's and 1890's is plausible but highly dubious. All these places are very isolated from the more southern range of deer both geographically and chronologically. For the more southern regions information is available for a period not later than the eighteenth or early nineteenth centuries, while finds of deer remains belonging to the first half of 1000 A.D. are known from Kaluga region (Tsalkin, 1956; for data on Pskov and Ladoga, see above).[69]

---

[67] Information about deer antlers found at Dubovka on the Volga and the deer hunting of the Kalmyks, according to Pallas (1776), pertains to reindeer and not to the species under description as is sometimes stated (Formozov, 1946), although Pallas erred in this case.

[68] That deer were brought into Moscow county not very long ago was first suggested by Turkin (1900), who saw with F.K. Lorents a relatively freshly shed antler found in the 1860's in Bogorod district (Bogorod now named Noginsk). This single evidence, even if it is reliable, cannot serve as proof. The possibility is not excluded that this antler belonged to an animal escaping that way. In Ismailov menagerie, for example, about 700 animals lived even in 1820's and were hunted (Middendorff, 1867).

There is no information whatsoever (except what has been given for Semenov basin above) about deer from the area between the middle parts of the Tambov and the Urals. Evidently the northern boundary of the range, running in mid-Russia somewhere around 54 to 55°N lat., proceeded eastward at the same level along the forest-steppe and farther toward the Urals. Here deer were reported on the western slopes not only in the upper reaches of the Sakmara (even in the first half of the last century), but also around Ufa (55° N lat.; end of eighteenth century, probably still later). The general direction of the range boundary of these deer bears a positive analogy to the boundary of the range of wild boar and roe deer.[70]

The extent of dispersal of deer in the Urals is not precisely known. Evidently, however, in the southern part of the mountain range they were widely distributed and inhabited the environs of Sverdlovsk on the eastern slope even in the first half of the last century and even in the 1850's (at 57° N lat.). It is highly possibe that west of the Urals the northern boundary was not restricted to 55° N lat.

From roughly 57° N lat. in the Urals the northern boundary of the range in western Siberia turned east with a slight southward dip, covering Barabinsk steppe from the north, and ran through the Mariinsk and Achinsk regions, i.e., roughly along 56° N lat. From there, rising slightly north, it turned toward the Yenisey, crossed Mendel' River, the left tributary of the upper courses of the Keta, and ran toward the mouth of the Angara, i.e., crossed the Yenisey roughly around 58° N lat.

In the region west of the Volga the range extended south up to the Black and Azov Seas and included the central Caucasian steppes up to the Caspian coast. The range there crossed directly into the
131 Caucasus where, toward the south, it extended up to the state boundary. Deer were probably absent in the desert areas on the right

---

[69] In Voronezh region, at Ramon', slightly north of Voronezh, deer survived up to 1917. After this they scattered, when Graf forest was colonized. Later a recent herd of deer from Voronezh sanctuary started settling there. One cannot state with certitude that Ramon' deer were indigenous forms and not introduced (at least partly).

[70] As in the case of roe deer, these deer too exhibit significant taxonomic differences between the western form, occupying western and central sections of the European part of the USSR (European deer), and the form associated with Siberia and the Urals (maral). Nevertheless, there is no adequate proof to suggest any effective isolation whatsoever between these regions.

banks of the lower Volga, but on the Volga itself were present up to Astrakhan'.[71]

The southern boundary of the reconstructed range between the Volga and Ural Rivers is not known. Based on physical conditions and ecological characteristics of the area and by analogy with some other ranges, one may only assume that the southern boundary probably passed somewhere between Stalingrad or Kamyshin and the Ural. There is reason to believe that in old times deer could have migrated far south, probably up to the Ural River estuary, along its bottomland deciduous forests.

Beyond the Ural River deer (maral type) were extensively distributed along the steppes of Kazakhstan,[72] and encountered along the bottomland deciduous forests of river valleys, along some islands of forest in the plains, and along some elevations and small hill sections. Their distribution there was confined to isolated spots, especially farther away to the south. The southern boundary of the range evidently covered the Ilek basin and passed via some unknown route through the upper course of the Tobol into the Aman-Karagay pine forest district (around 100 km south of Kustanay at Semiozernii).[73] From there the boundary turned through Kokchetau mountain into the Akmolinsk district, covered the distant Karkaralinsk mountains, and extended into Chingiz-Tau and then Tarbagatai. It is possible that the range boundary ran even more southward and covered the pine forest of Naurzum-Karagay (about 200 km south of Kustanay at Aksuat), and probably also the Ulutau mountains, and proceeded from there into the Karkaralinsk mountains directly to the east, but there is no direct proof of this.

In Middle Asia and southern Kazakhstan[74] the range (maral type deer) covered Tarbagatai, Saur, Dzhungarsk Alatau, and the entire Tien Shan mountain system in the south to the northern fringes of

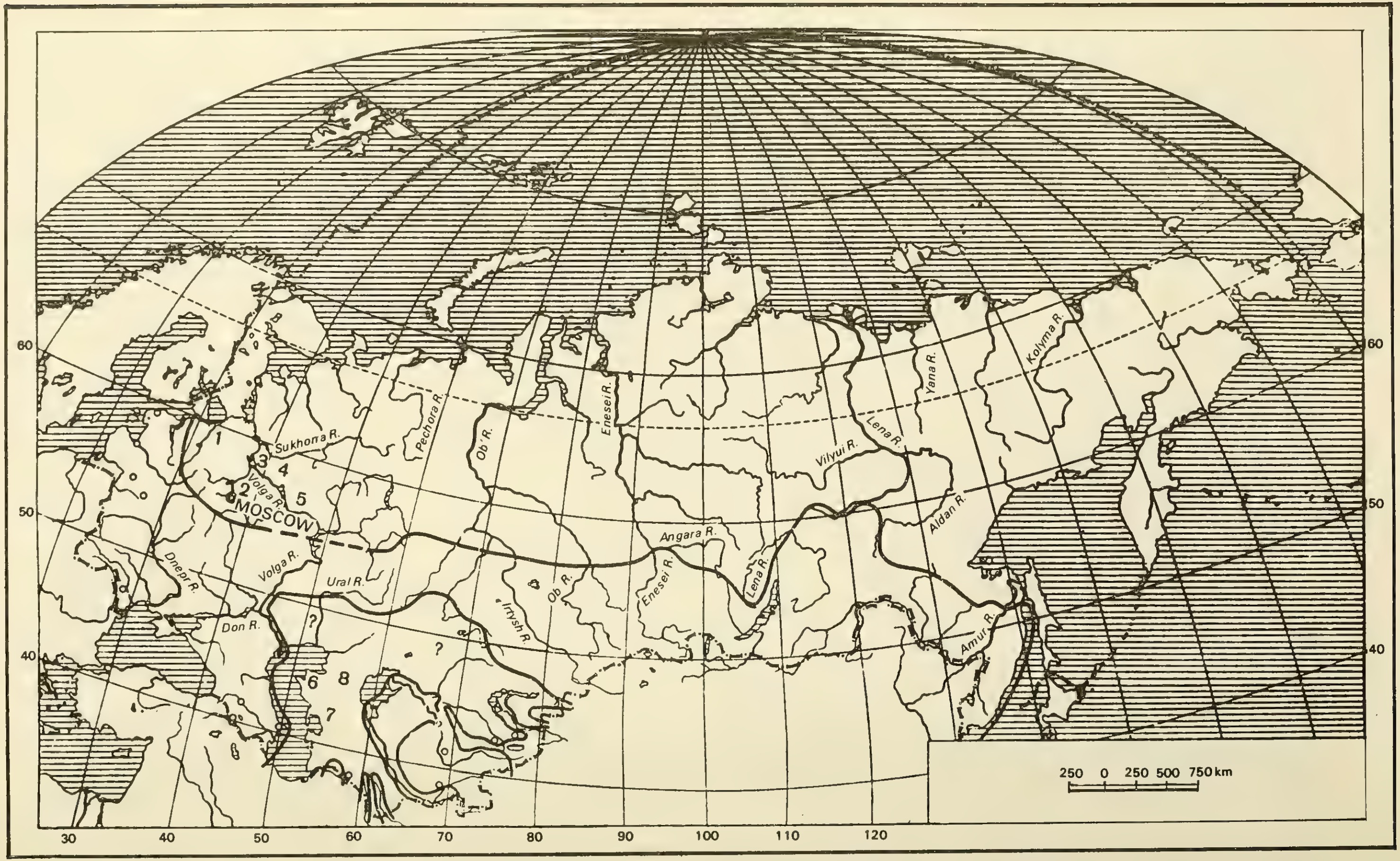
---

[71] The range and boundaries described are based on data of Middendorff (1867), Eversmann (1850), Pallas (1776), Ternovskii (1956), Turkin and Satunin (1900), and other sources, mainly from the literature and archive material gathered and processed by S.V. Kirikov.

[72] P. Rychkov (1762) wrote that maral is an animal of the steppes.

[73] Information about hunts by Tamerlane at An-Karagay in 1391 (S.V. Kirikov) evidently refers to this place.

[74] Of the individual finds in Kazakhstan reported by different researchers commencing from the eighteenth century, the following are mentioned: upper course of Ayat (left tributary of the Tobol), Bayanaul'sk, Kokchetau (Zeredinsk, Imantau, San-dytkav, Airtau, Maralsinsk, Sinyukhinsk, and Bol'shoi Toktinsk forests), Karkaralinsk, Eremeisk (Ermentau), Ken-Kozlak mountains, mountains of Bulga (Bugula), and Chingiztau (Kuznetsov, 1948; Antipin 1941; unpublished material of S.V. Kirikov).


60
50
40
1
2
3
4
5
6
7
8
?
?
MOSCOW
Sukhona R.
Volga R.
Volga R.
Dnepr R.
Don R.
Ural R.
Pechora R.
Ob' R.
Ob R.
Irtysh R.
Enesei R.
Enesei R.
Angara R.
Lena R.
Lena R.
Vilyui R.
Yana R.
Aldan R.
Kolyma R.
Amur R.
30
40
50
60
70
80
90
100
110
120
250 0 250 500 750 km

the Ferghana Valley and the northeastern extremity of the Alaisk range, in the west to Chatkal'sk and Talassk ranges, and in very old times probably also Ugam and Kuraminsk. The Trans-Iliisk Alatau and Aleksandrov (Kirgizia) ranges constituted the northern rim of this part of the range. Information on the penetration of maral farther north at the Chu-Iliisk ranges is not available, although it is possible that the animal did live there during very old times. It penetrated the Pri-Iliisk jungles, however, settled in the Ili estuary, and also survived in the Balkhash rushes (Turkin and Satunin, 1900). In the northwest the range extended up to the Karatau range.[75]

132 Apart from the regions described above there were some habitats in Middle Asia occupied by deer of different forms. Some were associated with the Syr-Darya and Amu-Darya. Along the Syr-Darya deer (Bukhara or tugai-type deer) dispersed along the tugais of river valleys all along the Aral Sea upward at least to Kzyl-Orda, but undoubtedly much higher in bygone times. There is, however, no positive information about this. Evidently deer were also distributed somewhat east of the river into the desert and probably penetrated the lower course of the Sarys and up to Karatau.[76]

[75] Information about deer in Karatau is reported by N.A. Severtsov (1873) in Kirgizia. Some later researchers doubted these data but without proper basis. Severtsov conceded that Karatau deer extended into Syr-Darya and suspected that Karatau and Syr-Darya deer belonged to a species other than that of the eastern parts of Tien Shan, i.e., they were not marals. Insofar as this concerned Syr-Darya, he was of course correct; it is impossible to resolve this question for Karatau deer which disappeared from there long ago. It is more probable, however, that this form was maral.

[76] Severtsov (1873) suggests that the range in Syr-Darya joined the habitat in Karatau along the extensive shrub lands which existed then; this is highly justified. Data for the Sarys were reported on the basis of conjectural and dubious information gathered by N.V. Pavlov (1931), although there is nothing improbable in them. The form of deer occurring there, whether maral or Bukhara, has also not been established. Either of the two could be assumed with equal justification.

---

130 Fig. 45. Reconstructed geographic range of red deer (*Cervus elaphus* L.) in the Soviet Union (scale in km). Question marks indicate uncertainty about the extent of occurrence of *Cervus elaphus bactrianus* Lyd. in the Ural valley, Ulutau district, and Syr-Darya valley. Broken section of line indicates suggested northern boundary in regions for which there is no information.

1—finds of remains at Old Ladoga (beginning of first millenium A.D.); 2—finds of roughly same period around Moscow and dubious information about finds in 1860's; 3,4, and 5— extremely dubious, evidently erroneous references about Nikol' basin district of Vologod province, Galich-Kostrom and Semenov-Nizhegorod for end of nineteenth century; 6, 7, and 8—erroneous references to Sary-Tash and southwestern and northern Ustyurt for 1930's. V.G. Heptner.

Farther away the range covered almost all of the Kyzylkum which, until recently, was extremely rich in saxaul. In winter and spring, having moved out of the valleys and deltas of the Amu-Darya and Syr-Darya, deer scattered widely not only in those parts of deserts which directly adjoin the river valleys and Aral Sea, but also in extremely far away places, at least in western and northern parts of the desert. It is highly probable that in the growth season of ephemeral plants tugai deer from the Amu-Darya delta could move out for a small distance into the desert in the adjoining parts of the Ustyurt and the Aral Sea coast as they did in northern Kyzylkum, where the environment was more favorable to them (saxaul forest).

Along the Amu-Darya deer moved to wherever reed and tugai thickets were available, from the estuary to the source of the river in the mountains, i.e., roughly up to 70° E long., to the south or southeast of Kulyab. In the upper reaches of the Amu-Darya deer dispersed from the river along the tugais, in all of its right-hand tributaries, from Shirabad to Kyzyls wherever tugais were present, i.e., quite far away during olden times. They were confined, often only during some seasons, to interfluves between the tributaries of the Amu-Darya and the mountains, especially in Babatag. The possibility of deer having reached the foothills of the Gissar range and Darvaz mountains has not been excluded although there is no information about this.[77]

It is possible that deer (probably of the tugais type) lived along the Murgab but it must have been long ago and there is no positive information about this. Deer (probably Caucasian type) lived along the Tedzhensk and in Kopet-Dag in the southeastern part in the Atrek basin, which penetrated along girkan-type topographic segments from adjoining Iranian regions (Caucasian deer).[78]

---

[77] Turkin (1900) describes in great detail, citing no references whatsoever, an altogether unbelievable geographic range for deer in the region south of the Syr-Darya. Part of the range described by him evidently pertains to Marco Polo's sheep but his references to forests (in eastern Pamir! V.H.) are confusing.

[78] The southern boundary beyond the Volga and the geographic range in Middle Asia are based on material from Severtsov, 1873; Kuznetsov, 1948 and 1948a; Shnitnikov, 1936; D.P. Dement'ev, 1938; Bazhanov, 1945; Antipin, 1941; Zarudnyi, 1896; Flerov, 1935; Turkin and Satunin, 1900; Heptner, 1949 and 1956; and other sources; and also original material of V.I. Chernyshev and V.G. Heptner.

There is a report (Bazhanov, 1945, based on material gathered through questionnaires) that deer were observed in the northern (!) part of the Ustyurt desert (1935), in the Sarytash (Sary-Tas) region on the Caspian Sea coast deep inside Mangyshlak Gulf region (summer of 1940 and winter of 1941-1942) and that, 200 years ago, according to the accounts of "old people" (! V.H.), deer were common in the large saxaul forests of

133 In Trans-Yenisey Siberia and in the Far East the range of deer (in the west—maral, and in Trans-Baikal—Manchurian wapiti) revealed the following characteristics. Commencing from the mouth of the Angara the northern boundary of the range ran along its left bank to the mouth of the Chuna (Uda) and along the Chuna southeast roughly up to Vydrinsk (Vydrino-Berezovaya). From there, turning east, it extended into the Angara approximately in the region of Ust-Vihorev and descended southeast into the source of the Lena River, roughly toward Kachuga and Anga. From there the boundary, running for some distance from Baikal and including Baikal in the range, turned almost directly northward. North of Baikal it encompassed the Chai basin, at least its upper reaches, the Little and Great Chui and Vitim (i.e., northern Baikal and Patom foothills) and emerged at the Lena slightly east of Mukhtuya at 114° E long. From there it proceeded along the left bank of the Lena for some distance and reached 61° or even slightly more north (northernmost point of habitation of deer in the Soviet Union). Along the left bank the boundary extended to a place 100 km above Olekminsk, continued to the right bank of the Lena, and proceeded along it to a place 100 km below Olekminsk. From there the northern boundary of the range sharply descended south through the uppermost reaches of the Amga, ran slightly west of Aldansk town, and emerged through the Chul'mansk (at the source of Timptonsk) toward Stanovoy range.

The location of the boundary between the above portion of the Stanovoy range and the Amur is not altogether clear in some respects. Evidently it ran initially along the southern slope of the Stanovoy range, especially along the source of the Gilyuya and its upper tributaries, and later descending slightly southeast turned through the source of the Uda River, upper reaches of the Selemdzha, source of the Bureya, and upper reaches of the Amgun, intersecting them, to the mouth of the Gorin, entering the Amur from the left. On the right bank the boundary passed through the mouth of Khelasso River (? V.H.; 51° N lat., i.e., slightly below the

---

southwestern U styurt and are at present quite often encountered in the Great Balkhan mountain regions. These data are hardly factual and highly incredible. Nor can one accept the taxonomic status of these animals, their migration, etc. which the author bases on such reports. It can, for example, be demonstrated that over the last few decades deer have only very rarely entered Kopet-Dag and the extreme southwest at the exact boundary with Iran (one reliable instance is known; Heptner, 1949). Deer were obsent in the well-investigated Great Balkhans and there is no positive information whatsoever about their past occurrence. Information about roe deer in the Great Balkhans, reported by Bazhanov, is therefore considered erroneous.

mouth of the Gorin). East of here the range covered parts of the basins of Amur tributaries, the Yaya, and Tumnisk, the latter falling into Tatarskiy Strait (?—Tumdshi according to Schrenk, 1859). Toward the ocean the boundary terminated at De-Kastra Bay (about 51°40′).[79]

South of the range boundary outlined above deer reached the state boundary everywhere and crossed it. Exceptions were the steppe and semisteppe zones in southeast Trans-Baikal where this species was evidently absent.

Present Geographic Range in the Soviet Union

The present range of deer in the Soviet Union (mid-1950's) differs sharply from the reconstructed range, the former constituting only a small part of the latter. Moreover, instead of a continuous or relatively continuous range, we now have only one fairly massive zone in the east and small sections in other places. Furthermore, at several places where deer are now encountered, they are not indigenous; the animals were introduced in preserves or game farms under the protection of conservation measures far more stringent for deer than for other game ungulates.

In the west deer are often seen in game farms of Latvia (Tsirava, Mezhatne, Bukaishi, Valmere, Dene, Vitsgulbene, and some other places). These animals were introduced before the First World War from Belovezh Forest and later from other places (Germany). In Estonia there are a few animals living on the Abruk islands (southern coast of Sarem Island) and in Audr forest (northwestern Pyarn), which are descendants of animals introduced after World War I from 134 Germany, which died out in other parts during the Second World War. Only a few animals have survived in the Audr region (E.V. Kumari; data for 1957).

In Lithuania deer (of the same origin) are seen on the right side of the Nemansk in regions located in the northern parts of the republic.[80] Some animals are also present in Kaliningrad region (animals of game farms) but there is no definite information about them.

---

[79] The boundary of the range beyond the Yenisey is based on data from Middendorff, 1867; Maak, 1859; Schrenk, 1859; Gassovskii, 1927; Abramov, 1954; Kopylov, 1948 and 1950; Podarevskii, 1936; Favorskii, 1936; and unpublished data from D.U. Ivanov (Yakutia).

The sharp deflection of the range boundary from the Stanovoy range to the south and the detour of Uda and Amgun basins has been explained by old and recent researchers as due to heavy snow in the east.

[80] These regions number eight: Ionishkis (northernmost), Yurbarkas (adjacent to Kaliningrad region), Kurshenai (west of Shaulyai), Pakroiis (east of Shaulyai), Tauroge (lower course of Nemansk), Zhagare (near Ionishkis), and three regions on the left bank of the Nemansk (F.L. Ivanauskas; data for 1957).

In Belorussia deer exist in three areas: Belovezh Forest (between Grodno and Brest at 24° E long.), Volozhinsk region (south of Molodechno), and Ivenets (west of Minsk). Present-day Belovezh deer originated from animals introduced from Germany in the middle of the last century (Sileziya, 1865); other deer were introduced there even later. Deer of Volozhinsk and Ivenets regions are also introduced forms (1929), probably from Belovezh (Serzhanin, 1945).

In the Ukraine the single natural locale of deer is the Carpathians. This is quite a large massif associated with forests and high altitudes; the area occupied by deer is quite extensive, corresponding to the elongated stretch of the mountain range. In the east this segment commences in the Putil'sk (Putila) region south of Chernovits at the Rumanian border; in the west it runs toward the border with Poland and Czechoslovakia between Drogobych and Uzhgorod. The boundary of this segment extends from Putila along the Rumanian border in the west up to a point south of Rakhov in Tissa.[81] Another locale of deer in the western Ukraine is situated north of the one described above. It is in the form of a belt extending from west to east along the border with Belorussia, almost from the Polish border roughly from the source of the Pripyat to the Stviga (right-hand tributary of the Pripyat, slightly west of 28° E long.). It thus covers the region northwest, north, and northeast of Kovel, to the north of Lut and north-northeast of Rovno. The southern boundary of this belt traverses roughly in a straight line slightly north of Kovel-Rafanovka-Sarna, the border between the Ukraine and Belorussia, forming the northern boundary in this segment.[82] The origin of these deer is not known but there is no doubt that they are not natives but probably represent animals escaping from Polish game farms.

There is a fairly large population of native deer in the forests of montane Crimea[83] and an altogether isolated colony exists in Voronezh preserve (forests north of Voronezh), evidently representing deer brought from Europe (see footnote 69 above). Small groups of deer are present in a wild or semidomesticated state in Askaniya-Nova, in the floodplain of the Dnieper at Goloi Pristan and Burkutakh (about 35 km east of Goloi Pristan), in Azov-Sivash preserve (Biryuchii Island in the Azov Sea, east of Genichesk) and in forests of the Pechenezh region (Pechenega) about 50 km southeast of Kharikov. Deer of no particular breed were brought from Askaniaya-Nova to inhabit the last five places and represent a heterogeneous population of different forms of species *Cervus elaphus* (European and Crimean deer, maral, and Manchurian and American wapiti) and even sika deer.

---

[81] This segment is located in the regions of Volovets, Svalyav, Irshav, Mezhgor, and Rakhov of Trans-Carpathian district; Slav, Khyrov, Starosambor, Turkov, and Borinsk of Drogobych region; Nadvornyansk, Yaremchansk, Zhabov, Dolinsk, Bolekhov, Peregonsk, Kosov, and Vygod of Stainslav district; and Brodov (Brodov forests) of L'vov district (Tatarinov, 1956).

[82] This zone extends to the Olits region of Volynsk district, to Derazhnyansk and Sosnov in Rovensk district. It is quite natural to suggest that deer should be encountered even in adjoining sections of Belorussia, but no information whatsoever is available about this (Serzhanin, 1955). It is possible that they reach the Polish border in the west.

135 In Mordov (north of Temnikov at Mokshe), Khoper (on Khoper River at Novokhoper), Bashkir (west of Magnitogorsk), and Il'men preserves maral were acclimatized.[84]

Deer occupy a considerable area in the Caucasus. This is a native animal existing within the confines of its natural range, is protected, including several sanctuaries, which in total area are no larger than legally prohibited areas.* Earlier the range was invariably continuous and extensive and included all the forests of the country; now as a result of shrinking forest areas and persecution it has shrunk considerably and has broken into several fairly large isolated areas. Although some increase in the population of deer has occurred in the last decade and an enlargement of the area of habitation has been observed in some parts of the country, a considerable shrinkage of the range compared to that of the early twentieth century is still discernible.

At present the largest segment of deer habitation in the Caucasus falls in the forest regions of the western part of the mountain range, i.e., both northern and southern slopes in the area between Krasnodar (about 39° E long.) and almost up to Elburz (about 42°30′ E long.). Here, in the north, deer almost reach Maikop and, in the south, the range boundary extends slightly short of the sea. On the whole the outlines of this part of the range form an irregular triangle with the peak pointing northwest.

---

[83] The suggestion that Crimean deer came from animals brought by the Crimean Khans is hardly justified. Taxonomically Crimean deer are quite independent and occupy an intermediate position between Carpathian (*montanus* Bot.) and Caucasian (*maral* Og.) deer.

[84] Maral live in all the listed sanctuaries and have dispersed quite far away from Il'men. But their fate in the territory of the now disbanded Bashkir preserve is not known; it is possible that they have died.

In the 1950's especially the mid-fifties, hunting organizations introduced quite a large number of deer, mostly maral but partly Askaniya hybrids into quite a number of places. Thus maral were introduced into some places of Moscow district and even into Estonia. Information about these introductions is very scanty and hence not included here.

*Meaning of passage not clear in Russian original—General Editor.

In the east deer occur in the forest zone in the northern foothills and the low mountain belt from Nal'chik to Groznyi (46° E long.). Some parts of the habitat lie along the Terek on the plains, where deer occupy bottomland deciduous forests and Caspian reeds from a place slightly below Gudermes. They are also encountered among reeds along the lower course of the Sulak and its estuary.[85]

Deep inside the mountains on the eastern extremity of the mountain range there are sections of deer habitat in the upper reaches of the Avarsk Kois and Samur. There is also an isolated part of the range in the forest region facing the Caspian Sea on the low belt of mountains between Makhachkala and Derbent, more accurately slightly south of Makhachkala and up to the Samur estuary.

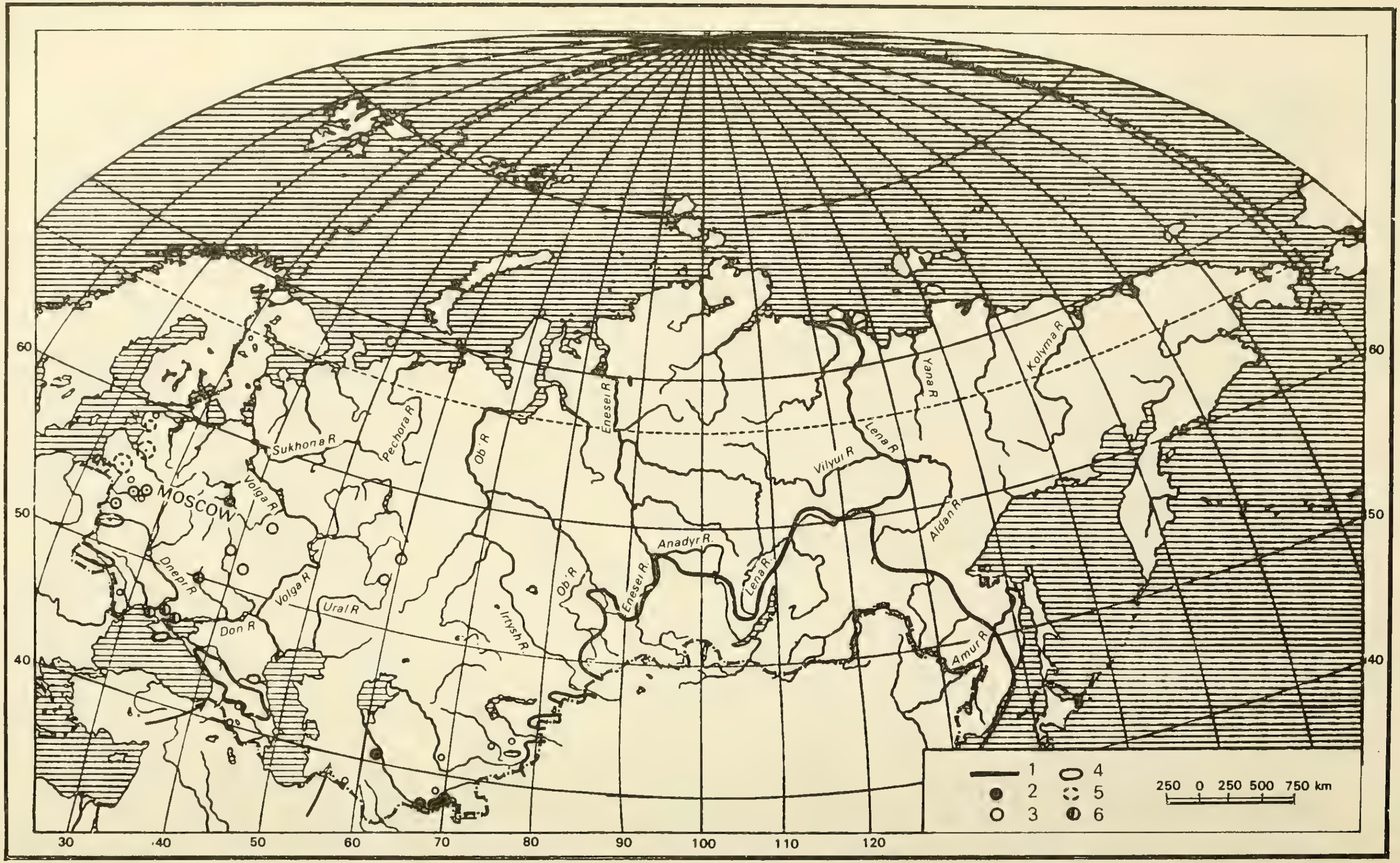
In Trans-Caucasus the range of deer extends as a long narrow belt through forests on the southern slopes, approximately from 48° E long. on the east to Lagoda (about 46° E long.) on the west. A small part of the habitat occurs in the Kur' valley to the southeast of Tbilisi, and another of the same size, or slightly larger, north of it, and a fairly large one to the west. The last is in the form of an oval with the center at Borzhom and is located along Trialet and Imeretinsk mountain ranges. Finally, there is an extremely small section southeast of Batumi into which animals probably penetrated from Turkey.[86]

Deer are absent at present in the Urals and in much of western Siberia (excluding maral acclimatized in Bashkir and Il'men preserves). Their range beyond the Urals covers eastern Siberia and the Far East and commences in Altai and in regions north of it. In the southwest the boundary commences at the state boundary to the northeast of Lake Markakol'. Running west and northwest it
137 encompasses the upper Bukhtarma, i.e., southern Altai and Listvyag ranges and the southeastern part of Kholzunsk, roughly at the source

---

[85] The position changed in the mid-1950's due to the drying up of Caspian Sea and recession and destruction of reeds.

[86] The description of distribution in the European part of the USSR and in the Caucasus is based on data from Kalinin'sh, 1950; Serzhanin, 1955; Tatarinov, 1956; Korneev, 1952; Vereshchagin, 1947; Heptner and Formozov, 1941; and others.



MOSCOW
Sukhona R
Pechora R
Volga R
Dnepr R
Don R
Ural R
Ob' R
Irtysh R.
Enesei R
Anadyr R.
Lena R
Vilyui R
Yana R
Kolyma R
Aldan R
Amur R
30
40
50
60
70
80
90
100
110
120
1
2
3
4
5
6
250 0 250 500 750 km

of the right-hand tributary of the Bukhtarma-Khamir. From there it turns north-northeast and, encompassing the Terektinsk range, leaves the Katun somewhere south of Gorno-Altaisk (Oirot-Tura and Ulala), probably at the Chemal or slightly north of it. From there the boundary runs to the midcourse of the right-hand tributary of the lower Biya-Lebed.[87] In the extreme south of Altai the range does not reach everywhere directly up to the state boundary; for example, the Chuisk steppe is not part of it.

To the north from the Altai (Lebed') the boundary turns steeply north, making large loops and encompassing Salair principality and the Kuznetsk Alatau. In the principality the range reaches roughly up to 54°30′ N lat. and, moving slightly west, its extreme western point falls roughly at 85° E long. In the Kuznetsk Alatau the range reaches up to 55° N lat. and is bounded by foothills to the east (roughly 90° E long.). Beyond approximately 53° N lat. the boundary turns east sharply, runs along the right bank of the Abakan and then the Yenisey, and ascends sharply northward (Yanushevich and Balagoveshchenskii, 1952; map).

The northern boundary of the range east of the Yenisey, i.e., in eastern Siberia and the Far East, corresponds to the range described

---

[87] Detailed information about the geographic range in the Altai has been given by Dmitriev (1938) for the 1930's. From that time the range has become somewhat enlarged at places, probably quite considerably, i.e., it may be assumed that this enlargement did not occur exclusively in the region of the upper Bukhtarma (E.I. Strautman, 1953). Nevertheless the range in Altai as outlined by Yanushevich and Blagoveshchenskii (1952) appears somewhat exaggerated; the boundary just crosses north of Gorno-Altaisk almost at the confluence of the Katun and Biya. Boundary descriptions have been compiled from the foregoing references and data collected personally by V.G. Heptner.

---

136 Fig. 46. Present (mid-1950's) distribution of red deer (*Cervus elaphus* L.) in the Soviet Union.

1—northern boundary of distribution of native deer of central and eastern Siberia and the Far East: maral (*Cervus elaphus sibiricus* Sev.) and Manchurian wapiti (*C. e. xanthopygos* M.E.); and geographic range boundaries of Tien Shan maral (*C. e. songaricus* Sev.), Caucasian deer (*C. e. maral* Gray), Crimean deer (*C. e. brauneri* Charl.), and Carpathian (*C. e. montanus* Bot.) (range of Caucasian deer extremely generalized and schematic); 2—locations of natural distribution of Bukhara deer (*C. e. bactrianus* Lyd.); 3—some places of successful acclimatization of maral in the last decade; 4—location of occurrence of naturalized introduced European deer (*C. e. hippelaphus* Erxl.) in Belorussia and in northwestern Ukraine; 5—approximate places of distribution of the same forms in Lithuania, Latvia, Estonia, and Kaliningrad; 6—some habitations of polyhybrids of Askaniya origin. Arrows indicate places of transgression of deer into western Kopet-Dag and southeast of Batumi. V.G. Heptner.

before (see reconstructed range). There is no information about the occurrence of deer in this vast territory for the past few centuries. The earliest data go back only to the middle of the last century. In any case there were no adverse variations of the range boundary. Based on stray facts and some general tendencies one may even assume, on the contrary, that deer advanced in the last decade even farther north in northern Baikal and Yakutia. Only a small section of the range in the Far East underwent adverse changes. Now the boundary from the upper reaches of the Amgun runs not to the mouth of the Gorin but intersects the Amur above, at the mouth of the Sungari (right-hand tributary of the Amur) and from there, without encompassing the Yaya basin and Tumnin, runs directly southeast, emerging toward the ocean at the Samargi River estuary (about 47°20′; Abramov, 1954).

While the entire range boundary and its general outline beyond the Yenisey have not undergone major changes, there are considerable parts of the territory inside the range which are not colonized by deer at present. It is not possible to list and describe all of them. Attention may be drawn to the sporadic distribution of the animal in northern Baikal, in the large zone along the railway track in Irkutsk where there are no deer, and some other areas in eastern Siberia and the Far East. Throughout this land red deer are distributed generally less uniformly than roe deer and elk.

138 In Middle Asia and Kazakhstan the range has undergone extremely distinct changes and has shrunk notably. In all the steppe zones of Kazakhstan in the east, including Chingiztau, deer have disappeared totally. At present they are still encountered in the Tarbagatai, Saur, and Dzhungarsk Alatau.

The present distribution of maral in the Tien Shan is extremely limited and difficult to establish. Maral are absent in most parts of their former range except for a few places; they are few in number and distributed sporadically; at places they are rare and encountered singly. Maral live in the Ketmensk range (upper reaches of the Kena, Kegensk range) and in the eastern parts of the Kungei-Alatau (Tyup River basin). From the upper reaches of this river the boundary of maral distribution runs southwest and passes slightly east of Przheval'sk, encompassing the eastern parts of the Tersk Alatau. From there it proceeds in the same direction to the source of the Malyi Narym and the upper reaches of the Narym (above the mouth of the Malyi Narym) and to the source of the Atbasha, swinging sharply southeast later and running toward the Chinese border. This line forms the western boundary of the maral range in the Tien Shan (A.I. Yanushevich, data for 1957).

On the Syr-Darya deer are altogether absent at present; on the Amu-Darya only a small area is occupied in its midcourse at Darganat at 41°30′ N lat. (former Darganat preserve) and three small isolated segments in close proximity in the upper reaches of the Amu-Darya and along the lower Pyandzha and its tributaries. These sections are as follows: 1) along the lowermost reaches of the Kyzyl-su from a place northwest of Parkhar up to its mouth, and along the Pyandzha from a point east of Parkar below up to the mouth of the Kyzyl-su; 2) along the Vakhsha from Dzhilikulya and slightly north to the mouth and along the Pyandzha slightly above the mouth of the Vakhsha; and 3) along the Amu-Darya valley from a place slightly east of the mouth of the Kafirnigan on the Amu-Darya up to the boundaries of Tadzhikistan with Uzbekistan (about 67°40′ E long.) and away from the river (in the north up to Aivadzh) (according to V.I. Chernyshev).[88]

Deer were absent along the Murgab in antiquity; they were also absent along the Tedzhen, the references of some researchers notwithstanding (the latest available information pertains to the 1880's). Deer could only penetrate occasionally to the Kopet-Dag and that, too, only on the extreme border of the range, i.e., extreme southwest (V.G. Heptner).[89]

Geographic Range outside the Soviet Union

The range outside the Soviet Union (reconstructed) in the Old World included Algeria and Tunisia, probably Morocco (information about Senegal-Gambia erroneous), Corsica, Sardinia (evidently absent originally in Sicily, Crete, Cyprus, and islands in the Aegean Sea), the British Isles, western, central, and southern Europe, and southern Scandinavian Peninsula, i.e., in Norway roughly up to 65°

---

[88] The disappearance of deer along the Amu-Darya and Pyandzha, which rapidly continues even now, is associated with the destruction of tugais. Thus, even in the 1920's and early 1930's tugai deer were dispersed extensively along the lower Pyandzha and upper course of Amu-Darya. They inhabited areas from some points at 69°40′ E long. (Chubek, Moskovskii) to places slightly above Termez (border of Uzbekistan and Tadzhikistan). Along the Kyzyl-su and Yakhsu they reached Kulyab and Bal'dzhuan, along the Vakhsha up to Kurgan-Tyube and slightly more north, and along the Kafirnigan dispersed north of Shaartuz. Neither along the Surkhandar'e nor in Babatag and Karatau (a small elevation at Pyandzha) were they present in those years. The zone of habitation along the river was not continuous (Flerov, 1935; V.I. Chernyshev and V.G. Heptner).

[89] See p. 174 ff. for further information about the distribution between Caspian Sea and Amu-Darya.

N lat. and in Sweden on the Baltic coast up to 59° N lat. The range covers Asia Minor, northern Iran, Afghanistan (evidently only the northern part of it), Kashgar (Tarim basin), eastern (Chinese) part of the Tien Shan, montane parts of Dzhungaria adjoining the USSR and Mongolia, northern Mongolia (Mongolian and Gobi Altai, Hobsogol mountains, Khangai, and Khentei), northeastern China in the west including the Great Khingan, east and southeastern China in the south up to Szechwan, Tibet (mainly eastern part), and Himalayas including the southern slopes (Kashmir, Sikkim, and Bhutan).

In America the northern boundary of the reconstructed range proceeded from St. Lawrence Gulf to the eastern extremity of Lake
139 Superior and turned northwest roughly to Great Slave Lake (about 60° N lat.); from there it ran southwest to the coast of the Pacific Ocean, roughly 50° N lat. Along the coast the range extended in a belt as far as California.

The southern boundary turned northward in the form of a straight line, bypassed Nevada, passed through Utah to the central parts of New Mexico, arced northward, and descended as a promontory into Texas, reaching south to roughly 32° N lat. From there the boundary moved northeast roughly into Missouri, descended southeast into northern Alabama and Georgia, and departed again northeast toward Massachusetts and St. Lawrence Gulf.

The above reconstructed range no longer exists. Relatively important changes occurred in the New World and the once extensive continuous range has now been reduced to a few isolated sections, for example, in Idaho, Montana, Washington, Manitoba, and others. Deer in general have survived only as a result of effective conservation measures. In view of the fact that extermination of deer commenced only from the days of European colonization, i.e., relatively recently, the outlines of their natural range can be reconstructed rather easily.

In the Old World history has affected the range in a different manner. Outside the USSR, namely in Europe, the general boundary of the range has altered very little. However, distribution, formerly fairly continuous (at the commencement of the Christian era), changed long ago. Deer are now found only in some small segments, mostly isolated and separated from each other. They exist only in game farms as strictly protected and nurtured animals, because they represent a favorite object of hunting in Europe (prized for several centuries and even now). Many forms of protection, raising, selection, and other aspects of game husbandry have been perfected in relation to deer in populated areas. All these measures have perceptibly altered the form of European deer over the centuries but nonetheless preserved them in this part of the range.

In Asia deer have disappeared completely at several places; in some their disappearance took place long ago (eastern and southeastern China) and in others relatively recently, i.e., during the nineteenth century or even in the nineteenth and twentieth centuries. In some regions (China, Tibet, and India) deer are not adequately protected and their range and population continue to diminish. In Tibet deer still survive in pockets only because they happened to colonize in sacred forests, public places, monasteries, etc. where hunting is forbidden. As in Europe, deer are mainly protected in Tibet because they constitute a "feather in the cap"* of human conservationists.

Deer have been introduced for acclimatization into many places in Argentina, Chile, the USA (Nebraska and Kentucky), Australia, and New Zealand. Mainly European deer (Germany, Balkans, and British Isles) have been imported, but a few North American animals have been included in these experiments. (V.H.)

Geographic Variation

Geographic variation among deer is great, the number of forms numerous, and the range of characteristics very broad.

The publication of special monographs (Heptner and Tsalkin, 1947; Flerov, 1952) notwithstanding, the race structure of deer has yet to be satisfactorily explained. Among the large number of forms
140 described and commonly accepted[90] evidently seven or eight can be found in the Soviet Union. They are distinctly separable into three groups, viz., western, Siberian, and Middle Asiatic, corresponding to the three types of antler forms (elaphoid, maral, and hangul) described above.

Western-Central-European or Elaphoid Group

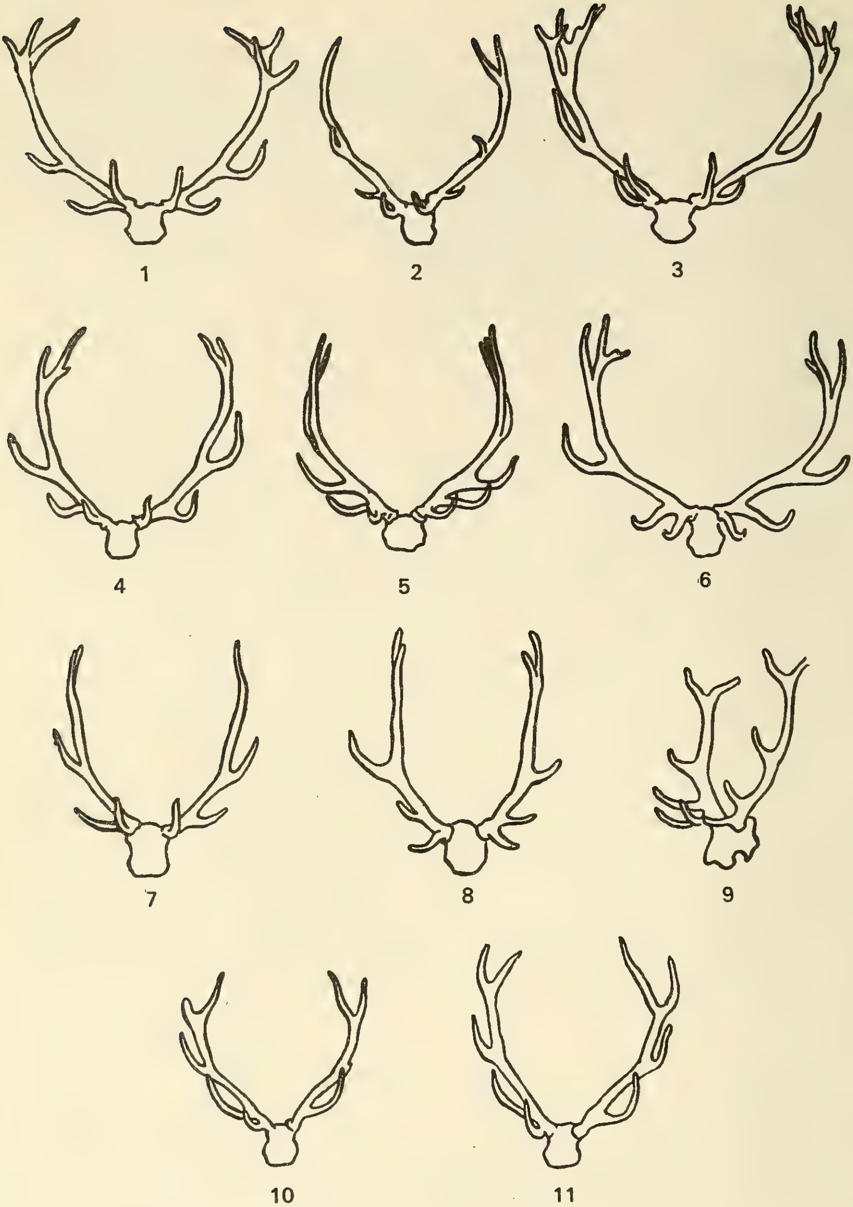
1. Central European deer [*C. (C.) e. hippelaphus* Erxleben, 1792].[91] Moderate size (height at withers 120 to 125 cm; stags weigh around 100 to 160 kg). Color of summer coat bright rusty-cinnamon (red

---

*Literal translation of Russian phrase is "fellow travellers of the culture"—Sci. Ed.

[90] Heptner and Tsalkin (1947) list 25, Flerov (1952)—13, Ellerman and Morrison-Scott—18 (1951), and Haltenorth and Trenze (1956)—15.

[91] Synonyms are numerous but none applicable to Russian fauna.



141 Fig. 47. Types of antlers of some races of red deer (*C. elaphus*) found in the Soviet Union.

1, 2, and 3—Caucasian deer (*C. e. maral*); 4, 5, and 6—Tien Shan maral (*C. e. songaricus*); 7, 8, and 9—Manchurian wapiti (*C. e. xanthopygos*) from Ussuri region; 10 and 11—Bukhara deer (*C. e. bactrianus*). Drawing purely schematic. From Heptner and Tsalkin (1947).

deer). Speculum brownish-rusty, rusty, or rusty-white, sometimes merging with color on the back. Winter coat dull gray, differing intensely from summer coat. Skull with narrow rostral portion; condylobasal length 375 to 410 mm. Antlers of moderate dimensions; number of tines more in this subspecies than in others and form a crown.

The range covers the western European part of the USSR except for the Carpathians. Outside the Soviet Union it covers central and western Europe (except the Scandinavian Peninsula), England, and Spain, and in the east extends up to Sudet[enland].

The difference between this form and the nominal Scandinavian form is slight and dubious. That the two forms are identical is highly probable.

2. Carpathian deer [*C. (C.) e. montanus* Botezat, 1903] (syn. *campestris* and *carpathicus*). Larger than preceding group and approach in their dimensions Caucasian deer. Predominant color more gray than that of central European deer; antlers very large and tend to be simple (many antlers without crowns).

The range covers the Carpathians. Outside the Soviet Union it extends over all of southeastern Europe east of Sudet[enland].

The independent nature of this form is dubious and many researchers place it as a synonym for the Central European form.

3. Caucasian deer [*C. (C.) e. maral* Ogilby, 1840] (syn. *caspius, caspicus,* and *caucasicus*). Large (height at withers about 135 cm). Coloration highly yellowish. Shoulders and thighs dark-colored. Sometimes summer coat of adults (females) with spots. Antlers large and heavy, sometimes with crown, and sometimes with two-tined fork. Number of tines on the average less than in European deer. Skull narrow but muzzle broader than that of central European deer. Condylobasal length of skull in males 433 to 460 mm; maximum skull length 472 mm.

The range covers the Caucasus. Outside the Soviet Union it includes the Caspian provinces of Iran and Asia Minor (?).

This form occupies a prominently intermediate position between European and Siberian races. Some researchers also place this form with the nominal race.

4. Crimean deer [*C. (C.) e. brauneri* Charlemagne, 1920] (syn. *tauricus).*[92] Moderate size, intermediate between European and Caucasian forms, but much smaller than the latter. Maximum skull length in males 335 mm (M 405.5) to 454 mm and in females 311 to 378 mm; condylobasal length of skull in males 320 to 437 mm and in females

---

[92] See footnote 63 above for significance of names given to Crimean deer.

302 to 378 mm. In the rest of their features Crimean deer are closer to Caucasian. Antlers relatively simple, number of tines usually not more than six, and crowns rare. In antler structure this form is very close to Caucasian deer and, together with it, occupies in this respect an intermediate position between western deer and eastern maral.

The range covers montane Crimea. These deer are absent outside the Soviet Union.

142 *Maral Group*

5. Altai maral [*C. (C.) e. sibiricus* Severtzov, 1872][93] (syn. *asiaticus, wachei, biedermanni,* and *baicalensis*). Very large, representing one of the largest races of the species. Height of stags at the shoulders up to 150 to 155 cm and weight up to 300 kg. Males in winter coat have a light gray-brown-yellow color on the sides; neck, shoulders, and abdomen darker than the rest of the body and cinnamon-brown. Females more uniformly colored and gray-brown. Summer coloration of both sexes a fairly uniform cinnamon-brown without darkening of neck, legs, and abdomen. Speculum large, broad, and high; descends onto croup; varies in color from dull rust to hay-yellow. Antlers very large, with a thick beam, without crown, and usually with six or seven tines. Fourth tine largest; at the point of its branching off the beam usually curves sharply to the rear (downward). Skull broad and muzzle wide. Condylobasal length of skull in males reaches 450 mm.

Newborn deer with body length of 92 to 101 cm, height at withers 74 to 77 cm, and weight in first week after birth 11 to 22 kg (Tsalkin, 1944). These fawns are thus larger than those of other deer races in the Old World.

The geographic range covers the Altai, Sayans, and Pri-Baikal region. Outside the Soviet Union these deer are found in northwestern Mongolia. The features of this form resemble those of some American forms.[94]

[93] Some researchers suggest that the name *sibiricus* Sev., 1872 has been preoccupied by the name *sibiricus* Schreb., 1784 given to reindeer and call the Altai maral *asiaticus* Lyd., 1898 or *baicalensis* Lyd., 1915. It is on this basis that Ellerman and Morrison-Scott (1951) gave the name *asiaticus* Lyd., 1898 (p. 369) to Altai maral. Yet, as explained by these very researchers (p. 376), the name *sibiricus* Schreber, in general has no significance whatsoever from a nomenclatural viewpoint, i.e., even in relation to reindeer, and they do not apply it to this species. Although in the situation under discussion there is an element of some misunderstanding, it is clear that the use of Severtsov's name *"sibiricus"* is entirely in order.

[94] Combining this form with the form *canadensis* of eastern Canada (Flerov, 1952) has no basis whatsoever from the viewpoint of taxonomy and is inapplicable and incomprehensible zoogeographically.

6. Semirechian (Tien Shan) maral [*C. (C.) e. songaricus* Severtzov, 1872] (syn. *eustephanus*). Large, corresponding in size to Altai deer, but with a slightly darker coloration of the trunk and limbs in the winter coat. Skull with retro-orbital walls somewhat narrower; width of occipital condyles and outer nasal orifice larger than that of Altai maral.

The range covers the Tien Shan and Dzungarsk Alatau. Outside the Soviet Union these deer are probably found in the eastern part of Tien Shan.

This is a poorly distinguished form and possibly identical with the preceding one.

7. Izyubr' [*C. (C.) e. xanthopygos* Milne-Edwards, 1860] (syn. *lühdorphi, isubra, ussuricus,* and *bedfordianus*). In body size somewhat smaller than maral and similar to Caucasian deer. Height at shoulders 145 cm and weight up to 250 kg; weight may be even more in some exceptional cases. Coloration in summer bright reddish-rust and in winter gray-brown-yellow. Speculum large and broad, in summer reddish-rust and only slightly lighter than the sides, and rust-colored in winter. Legs same color as trunk or only slightly darker. Antlers quite short and light with a relatively thin beam, set more or less straight. Crown absent and tines usually number six but sometimes only five. Fourth tine not particularly well developed and sometimes smaller than the rest. Muzzle between canines narrower than in maral. Condylobasal length of skull 390 to 435 mm.

The range covers Trans-Baikal and the Far East. Outside the Soviet Union these deer are found in northeastern and northern China.

This form is well differentiated. In Trans-Baikal its range adjoins that of Altai maral and animals with intermediate features have been described.

143 8. Bukhara deer [*C. (C.) e. bactrianus* Lydekker, 1900] (syn. *hagenbecki*).[95] Moderate or slightly smaller in size. In this respect Bukhara deer are similar to central European deer or even slightly smaller. Height at withers about 120 cm. Body coloration light yellowish-gray without rusty tones (sandy), being slightly more vivid in summer than in winter. Legs light-colored. Speculum well developed but approaching in dimensions that of European deer (smaller than maral and Manchurian wapiti); upper parts rust-

[95] This form of deer is sometimes known in literature as "hanglu," a popular name used for the related (or identical) form in Kashmir. Recently, it has been labeled "gavas," "govas," or "gavazd," or even pink (!) deer. There is no justification whatsoever to alter the very natural and fairly established Russian name and thus clutter up the nomenclature with foreign words.

colored or yellowish and lower parts whitish. Lips and underbelly white. Young (in first coat) differ sharply from young of other forms in having a light-colored general background. Antlers of medium dimensions, usually with five tines. Crown forms very rarely; two terminal tines generally bifurcate toward the sagittal plane of body, sometimes nearly at a right angle. Muzzle fairly broad. Condylobasal length of skull up to 390 mm.

Newborn fawns 56 to 60 cm high at withers, 78 to 86 cm long, and weigh on first day of birth 8 to 9 kg. They are thus significantly smaller than maral. Their main shade is much lighter than that of maral.

The range covers Turkestan. Outside the Soviet Union these forms are found in northern Afghanistan.

This subspecies differs very sharply from all other Russian forms. Its relation to the Kashmiri form *C. e. hanglu,* and through it to the Himalayan *C. e. affinis* needs to be accurately established. Closeness to the Kashmiri form is indisputable.

Outside the Soviet Union the following forms of the species are acknowledged: *C. e. barbarus* Benn., 1837 (northwest Africa); *C. e. corsicanus* Erxl., 1777 (Corsica); *C. e. hispanicus* Hilz., 1909 (Iberian Peninsula); *C. e. atlanticus* Lönnb., 1906 (Norway); *C. e. scoticus* Lönnb., 1906 (Scotland); *C. e. elaphus* Linn., 1758 (southern Sweden); *C. e. affinis* Hodgs., 1841 (eastern Himalayas and Tibet); *C. e. hanglu* Wagn., 1844 (Kashmir, probably identical to preceding form); *C. e. wallichi* Cuv., 1812 (southeast Tibet); *C. e. macneilli* Lyd., 1909 (central China, Szechwan); *C. e. alashanicus* Bobr. and Flerov, 1935 (Alashan, southeast Mongolia, northern Kansu, and Shansi); *C. e. merriami* Nels., 1902 (Arizona and New Mexico, USA); *C. e. nannodes* Merr., 1905 (California, USA); and *C. e. canadensis* Erxl., 1777 (rest of range in North America). The number of Asiatic and probably European forms in this list of Russian forms will no doubt be reduced in the future. (V.H.)

Biology

Population. The present-day geographic range of red deer in the Soviet Union is about one-half smaller than it was a few centuries ago. Deer are presently found in considerable numbers mainly in preserves and in a few regions in eastern Siberia and the Far East.

The current Baltic population of deer developed from animals acclimatized at different periods. In Lithuanian Soviet Socialist Republic in 1952 there were about 200 deer (Kuznetsov, 1954). This number had risen to 280 by 1955 (Ivanauskas, 1957) and to not less

144 Fig. 48. Crimean deer. July, 1955. Photograph by P.A. Yanushko.

than 300 by 1957 (F.L. Ivanauskas). At present, on the whole, the deer population in the Baltic region is not less than 400 to 450 animals.

In Belorussia deer are common only in the preserves of Belovezh Forest (72,000 hectares), where their 1953 population was 565 (684 in 1950 and 771 in 1951; Bannikov and Lebedeva, 1956). Until World War I, when Belovezh territory comprised 129,000 hectares (110,000 hectares covered with forests), deer were far more numerous—5,000 to 7,000 animals or more in 1907 through 1914 (Wroblewskii, 1912; Severtsov, 1940; and others), or 45 to 64 animals per 1,000 hectares of forest-covered area. These deer originated from animals introduced from western Europe.

In the Ukraine red deer are now most abundant in Trans-Carpathia followed by the Stanislav region; still their population as a whole in the republic (excluding Crimea) barely exceeds 1,000 to 1,200 animals.[96] Both native and introduced deer dwell here.[97]

---

[96] Including over 300 in Biryuchii Island in Azovo-Sivashsk preserve. These are hybrid Askaniya deer.

[97] For more details on acclimatization of deer, see the section below entitled "Economic Importance".

In Crimean preserve (30,000 hectares) in 1950 there were 2,096 deer or over 70 animals for every 1,000 hectares of land. In the rest of Crimea deer numbered 1,093 (hence, for Crimea as a whole, the total was 3,200), with density in different regions ranging from 0.7 to 16 per 1,000 hectares (highest in Alushtinsk and Kuibyshev regions) with an average of about 5.0 animals (Yanushko, 1957). Subsequently hunting deer was permitted in Crimean preserve and their population decreased. Then hunting was banned and the population increased to 2,224 animals in 1957 (A.A. Tkachenko).

In the rest of the European part of the USSR, excluding the Caucasus, deer are found in significant numbers only in the Voronezh region, where their population in 1952 exceeded 800 animals (Mertts, 1953). By 1955 the number of deer had risen to about 880 animals in Voronezh preserve alone (31,000 hectares), i.e., about 28 animals for every 1,000 hectares of land (Zharkov, 1957). Due to a drop in numbers in the severe winter of 1955 to 1956 and catching for purposes of acclimatization, the number of deer decreased (648 animals were counted in 1956 in Voronezh preserve, 448 in 1957, and 496 in 1958; P.F. Kaznevskii).

In the Caucasus the maximum number of deer formerly lived in Caucasian preserve. In 1939, when the territory of the preserve comprised about 300,000 hectares, there were up to 2,880 deer in it (Zhar- 145
kov, 1940). Following a reduction in the area of the sanctuary in 1951, conditions for deer worsened and, in subsequent years, their number in western Caucasus decreased. In Trans-Caucasus the maximum number of deer occurred in Trans-Katal and Lagoda preserves (over 1,000 animals in all) and in the territory of Borzhom preserve (there were 1,404 deer in 1943; Z.S. Ekvtimishvili; now probably less).

A small population of maral live in the southern Ural. Maral were introduced there in Bashkir preserve in 1940 to 1941; in 1951 they numbered about 350 (Kaznevskii, 1956).

Accurate figures are not available about the deer population of Siberia. They are found in maximum numbers in Altai preserve and are quite numerous at some places in the Sayans and Tuva Autonomous region. Until very recently they were common in the Baikal-Lena watershed region, in the upper course of the Lena and Kirenga, and at places along the left bank of the Angara. Deer were numerous in the Badaibinsk region of Irkutsk (Skalon, 1951) and quite common in Southern Yakutia where their population has even slightly increased in recent years (Belyk, 1953).

In the Far East the maximum number of deer occurred in Sikhote-Alin: their population was estimated as 10,000 in 1940 in

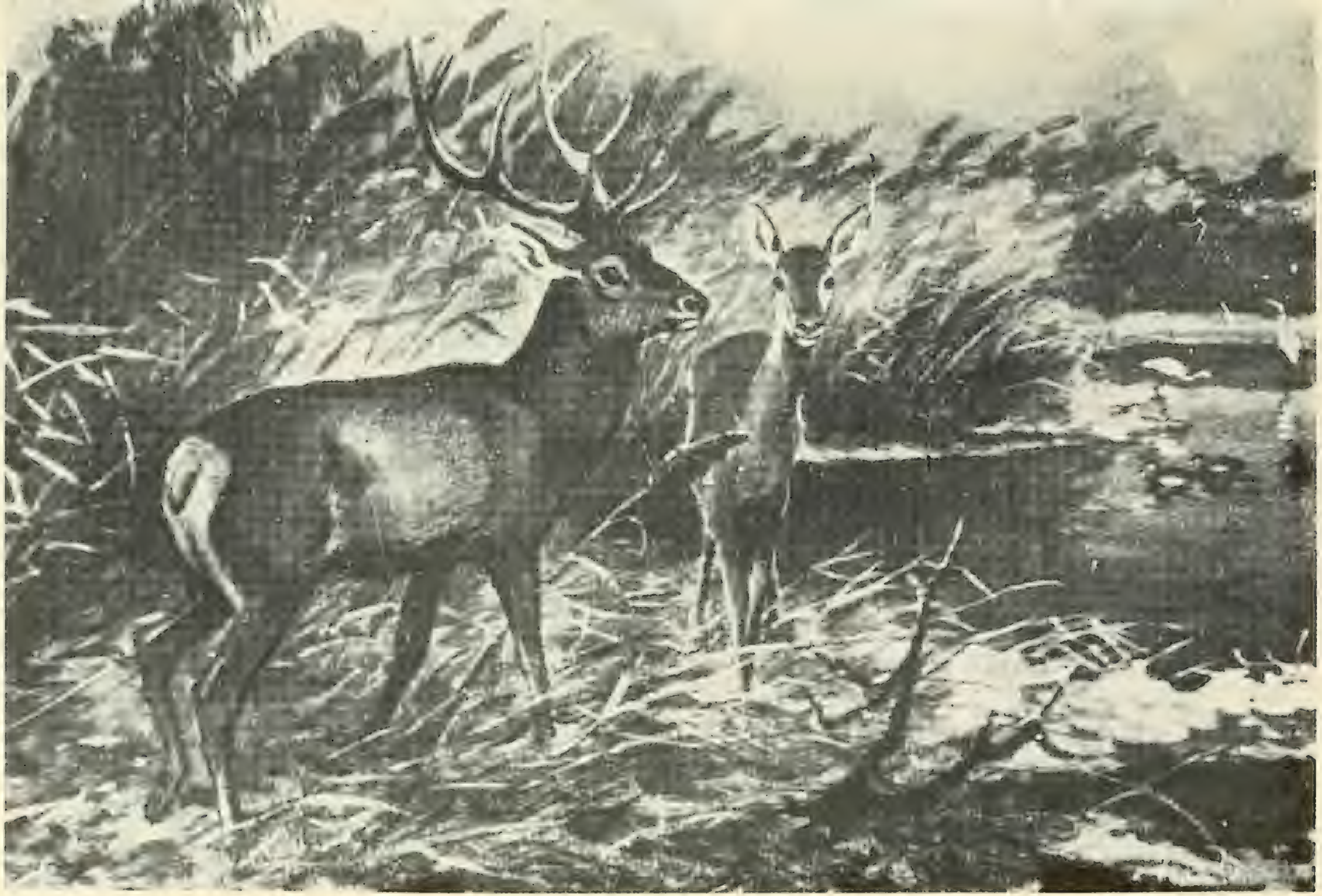


Plate 2. Bukhara deer. *Cervus (Cervus) elaphus bactrianus* Lyd. in summer coat. Drawing by A.N. Komarov.

Sikhote-Alin preserve (1,700,000 hectares) (Kaplanov, 1948). Following a reduction in the area of the preserve in 1951 the deer population decreased sharply.

Bukhara deer and maral are distributed in the territory of the Middle Asian republics. The maral population in Middle Asia does not exceed a few hundred. Bukhara deer have been protected mainly in the Amu-Darya basin—up to 100 animals in Darganatinsk tugais (Klyushkin, 1954; Dement'ev et al., 1956) and several hundred in Tigrovaya Balka preserve (23,000 hectares). In 1946 in the latter area 138 animals were counted and in 1949—222. Their number has recently increased to not less than 500 to 600 animals (Chernyshev, 1958).

On the whole the population of red deer in the Soviet Union comprises several tens of thousands of animals.

The former abundance of deer can be assessed with some caution from herd sizes, which are more or less proportionate to the total population and their saturation of the land. In Laba and Beloe basins, where the Caucasian preserve was later established, Dinnik (1910) sighted from the end of the nineteenth to the early twentieth century herds of 26 (Umpyr'), 35 or 36 (Bol'shoi Bambak), and 70 to 75 (Urushtensk) females; once he saw a herd of 13 males. Hunters have reported herds of 40 to 50 animals.[98] Over a five-year period, from 1933 to 1937, in Caucasian preserve only once were 30 deer sighted (in summer) in the upper course of the Kholodnaya; 20 of these (15 females and 5 juveniles) formed a single herd (A.A. Nasimovich).

Habitat. Their high ecological flexibility enables deer to survive under diverse conditions in nature from sea coasts to alpine or mountain tundra belts (in the Dzhungarsk Alatau mountains up to 3,000 m; Shnitnikov, 1936). The range of this species includes taiga and broad-leaved forest zones, steppes, and deserts (in semideserts and deserts, mainly in tugais along the banks of reservoirs and saxaul bushes), and also subtropical areas in the southern Soviet Union.[99] Thus deer inhabit not only regions with an extremely arid climate and snowless winters, but also areas with abundant rainfall and heavy snow in winter.

The extreme ecological plasticity of deer can also be judged from the results of successful acclimatization experiments with hybrid

---

[98] In Crimean preserve herds of 40 animals are sighted even now (Yanushko, 1957).

[99] In subtropical areas (south of Trans-Caucasus), as also in the steppes, deer at present are negligible.

146 forms (obtained by crossing Altai maral with Crimean deer having the blood of other forms) on Biryuchii Island in Azov-Sivash preserve, which reveals that they can survive even in the absence of fresh water (M.D. Shpigov).

For most of the year deer avoid evergreen and dense forest masses, preferring more sparse sections with an abundance of deciduous trees, shrubs, and herbaceous vegetation, and interspersed with meadows and glades. Especially convenient for deer life are places with a great variety of habitats. In the past, evidently, unusually large numbers of deer were encountered in the forest-steppe. Depending on the extent of winter snow deer may migrate en masse into the forest in winter (in places where the winter is more snowy), or on the contrary congregate in the steppes (regions with a continental climate).

At present the main deer reserves are concentrated in montane regions since these animals have become extinct on the plains or have disappeared as a result of topographic changes. In the mountains deer inhabit diverse habitats and often are encountered on steep and highly rugged slopes which elk usually do not reach. In general, wherever red deer, elk, and roe deer are found in the same

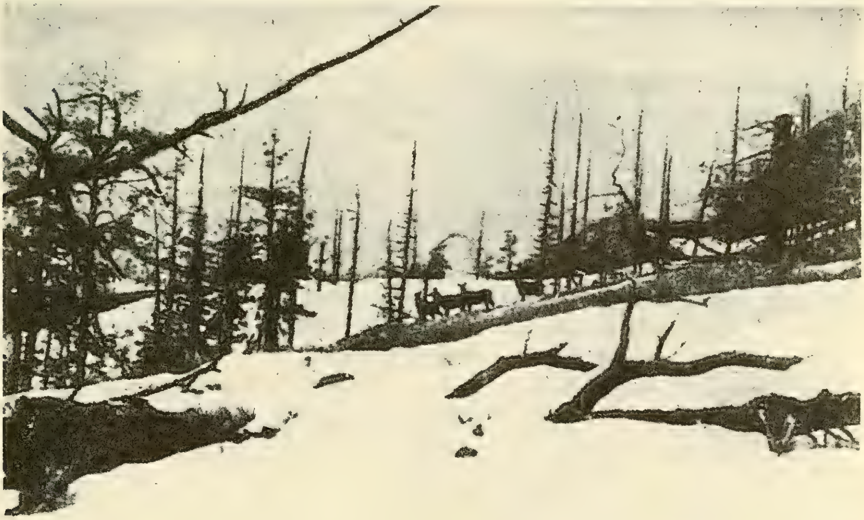


Fig. 49. Maral in spring on thawed patches. Bol'shoi Bashort range. Bashkir preserve. April, 1949. Photograph by P.F. Kaznevskii.

locality, red deer usually utilize a much broader range of habitats than the other ungulates.

Of special importance to deer life in the European part of the range are the following: in the Carpathians—beech forests from where deer often climb up to mountain meadows or glades (Tatarinov, 1956); in Belovezh Forest—abundant deciduous forests with undergrowth and herbage consisting of young pine and mature pine-fir-oak forests, or even alder forests in dry years (Sablina, 1955); and in Voronezh preserve—mixed and oak forests, and pine forests in winter if there are abundant shrubs and a leafy undergrowth (Mertts, 1951). In Crimean preserve in summer a maximum number of deer are seen in oak forests, followed by beech; in winter up to 95% of all deer sighted were located in oak forests (Yanushko, 1957). In the southern Urals maral acclimatized there are attracted to hilly pine-larch forest steppes and avoid evergreen, humid, and deciduous forests (Kaznevskii, 1956).

147 In Caucasian forests deer occur from the coastal rushes of the Caspian Sea (Dinnik, 1910; Heptner and Formozov, 1941) to high alpine meadows inclusive. In summer in Caucasian preserve deer are particularly numerous in the upper one-third of the forest belt (glades with tall grass vegetation, a zone representing the upper forest limit) and in subalpine and alpine meadows (up to 2,500 m).

In the Tien Shan mountains the main habitations of maral are fir forests interspersed with glades (Shnitnikov, 1936; Kuznetsov, 1948; and others). In southern Siberian maral and Manchurian wapiti use diverse habitats. Of special importance are burned-over forests with growing leafy seedlings and abundant grass. In montane regions the maximum number of deer are seen in the central parts of the forest belt of the mountains in the Altai and Sayans, and in the subalpine zone in summer from where they go even into alpine meadows. In the Sikhote-Alin mountains Manchurian wapiti abound in moderately old burned-over forests of the Manchurian and Okhotsk type and also in coastal oak forests. They are considerably fewer in coniferous forests. In summer some animals ascend to montane meadows at a height of 1,700 m (Kaplanov, 1948).

In montane regions (Caucasus, Altai, Sayans, and Sikhote-Alin) adult males are confined to the mountain slopes at slightly higher altitudes than females and young. However, in Caucasian preserve, in some habitats in alpine meadows, mostly females and young are seen in summer (upper courses of Kholondnaya) as well as in winter (Pshekish range) (Nasimovich, 1936 and 1955).

Extremely typical habitats of Bukhara deer are now mainly found in tugais of Amu-Darya basin. In Darganatinsk tugais deer are confined to prickly shrubs of the salt tree (*Halimodendron holodendron*), along sections with luxurious reforestations of poplar (*Populus pruinosa*), in bushes of oleaster (*Eliagnus angustifolius*) and in reed thickets. In summer deer are usually seen in association with an abundance of dense and high herbaceous vegetation and are frequently encountered in autumn and winter among forest plantations (Klyushkin, 1949 and 1954; and others). Along the Kafirnigan River deer inhabit a narrow belt of reed thickets with sparse bushes of oleaster. Along the Pyandzha and the lower reaches of the Vakhsh they occur mainly in flooded forests of swamp poplar mixed with oleaster. Particularly favored sections are small clearings with herbaceous vegetation and reed thickets (Bobrinskii, 1933; Flerov, 1935 and 1952; and others). In the cold season of the year Bukhara deer penetrate adjoining deserts, where they live in saxaul and tamarisk shrubs, avoiding extremely exposed and hilly areas (Flerov, 1935; and others). In the past they were found much more regularly in desert regions (Bobrinskii, 1933; Antipin, 1941; Bazhanov, 1945; and others). Migrations from tugais into adjoining deserts are also common in early spring, when ephemerals begin to emerge.

Bukhara deer differ notably from all other subspecies of red deer occurring in the Soviet Union, not only in relation to habitat but also in all other biological characteristics. These differences are much more significant than, for example, the corresponding differences between various species of turs.

Food. The food of red deer has been studied mainly in preserves; in general, no less than 300 plant species (including fungi) are consumed by deer, but detailed data have not been published so far. For Bashkir preserve over 150 plant species have been established as food plants for deer (Kaznevskii, 1954),[100] around 150 for Voronezh preserve (Mertts, 1953; and others),[101] over 130 for Crimea (Yanushko, 1957), not less than 80 for Belovezh Forest (Sablina, 1955; and others), over 70 for the Far East (Abramov, 1954),[102] about 60 for Caucasian preserve (Nasimovich, 1939 and 1940), over 50 for Altai preserve (Dmitriev, 1938), and up to 50 for Azov-Sivash preserve (V.A. Mattskov; M.D. Shpigov; Ishunin, 1956; and others). Data are even more scanty or altogether fragmentary for other regions.

---

[100] According to Danilov (1958) deer use in their food 234 types of angiosperms alone (61 types of trees and shrubs and 173 types of herbaceous plants).

[101] The full list of food plants has not been published.

[102] The full list of food plants has not been published. Kaplanov (1948) has listed slightly more than 40 plant species consumed by Manchurian wapiti in Sikhote-Alin preserve.

Of utmost importance in the plant food of deer are edible portions of trees and shrubs (branches, shoots, bark, leaves, buds, and needles of conifers) and fruits of some trees (beech, oak, etc.). In winter lichens are also consumed in some areas and horsetail in the Far East. Seedlings of reeds and saltworts are avidly eaten by Bukhara deer. Depending on the nature of the vegetation, extent of snow in winter, and numerical strength of ungulates, the frequency of herbaceous, tree, and shrub (branches) intake varies greatly.

Tree and shrub food are of great importance year-round, including summer, for deer in Belovezh Forest and especially in the Crimea. Thus in Crimean preserve food plants include 94 species of herbaceous plants and 37 trees and shrubs (81 and 27 respectively in summer). In the stomachs of six deer caught between May 27 and August 10 were found the remains of leaves, buds, and young shoots of trees and shrubs accounting for 60 to 70% of the total weight of food. In autumn and winter the remains of tree and shrub foods in the stomachs of deer comprise 60 to 85% of the total food mass (Yanushko, 1957).

Herbaceous, tree, and shrub food are of equal importance in the diet of deer in Voronezh, Bashkir, and Caucasian preserves. In summer mainly herbaceous vegetation is consumed. In Voronezh preserve tree and shrub vegetation and dried plant parts are mainly used in winter.[103] The food regime is roughly similar in maral of Altai preserve where herbaceous vegetation enjoys predominance in summer; in winter tree and shrub vegetation and dried plant parts are consumed to an equal extent.

In the diet of eastern Siberian deer, especially at places where winters are not extremely snowy (eastern Sayan, central Baikal, and Chita River basin), herbaceous vegetation is more important and deer consume it in considerable quantities not only in the snowless period, but also in winter, mainly in the form of dried plant parts (Pavlov, 1949; Kopylov, 1950; and others). Herbaceous vegetation is also extremely important in the diet of Far East Manchurian wapiti (Kaplanov, 1948; Abramov, 1954).

Depending on the season of the year and the availability of food resources, Bukhara deer consume fairly large quantities of herbaceous plants (wormwood [sagebrush] very avidly) or trees and shrubs (shoots of saxaul and tamarisk, poplar leaves, bark of young poplars, oleaster, and others) (Flerov, 1935; and others). In Darganatinsk tugais the most favorite and universal food of deer is the tender and succulent leaves of poplar (*Populus pruinosa*). These leaves are well consumed in summer as well as in autumn and winter when they shrivel and drop. Bukhara deer avidly take to the halophyte *Aeluropus litoralis* and, in early spring, ephemerals, especially desert sedge (*Carex pachystilis*) (Klyushkin, 1949). In the tugais of Tadzhikistan, Bukhara deer consume, apart from herbaceous foods, large quantities of tamarisk, saxaul, and saltwort in summer which, by autumn, become the main food; in winter, fruits of oleaster acquire utmost importance (Chernyshev, 1958). Succulent rootstock, bulbs, and other underground plant parts may play an important role in the ration of Bukhara deer, but this aspect has not been adequately studied.

---

[103] In Caucasian and Voronezh preserves fruits of nut-bearing trees are of vital importance in the winter diet of deer.

Azov-Sivash hybrid deer, because of sparse tree and shrub vegetation in the region, feed almost exclusively on herbaceous plants (legumes and grasses are particularly important). Often they eat common reed (*Phragmites communis*)—its tender shoots, succulent
149 and sweetish underground root stock, and tender flowering panicles still in their sheaths (M.D. Shpigov). In autumn roots of sea kale (*Crambe pontica*) and *Seseli* are avidly consumed; deer dig them up from the soil with their hooves (G.I. Ishunin).

One-eighth to one-fourth of the plant species consumed by deer can be considered the primary food taken in substantial quantity. For example, in Crimean preserve, of the 108 plant species used by deer in summer, 21 species are eaten avidly and often, 32 species to a lesser extent, and 55 species rather rarely (Yanushko, 1957).

Among herbaceous plants grasses are consumed regularly (their importance is particularly great in spring and early summer before their coarsening; they are also consumed in winter in large amounts). Other plants consumed avidly are those of families Compositae (including wormwood), Leguminosae, and Umbelliferae. When food is abundantly available, the most nutritive or succulent parts of herbaceous plants are used in the first instance; in the latter half of summer flowers and the upper parts of stalks are avidly eaten (western Caucasus, Belovezh Forest, etc.), and in winter the root portions of green stalks and the leaves near the roots of perennials. Grasses which remain green in winter (mountain fescue and others) represent the favorite food of deer in the Caucasus, Altai, and the Sayans. Deer eat good hay more readily than twiggy food. In spring forest squill, pasque flower, and some other early spring plants are consumed well. In Siberia a particularly favorite deer food in summer is buckbean; in northern Mongolia leeks are avidly consumed in autumn (Bannikov, 1954). Deer also eat belladonna, aconite, and other poisonous plants well.

From among trees and shrubs deer in general use no less than 70 species; of particularly great importance are oak, some maples, elm, ash, hornbeam, witch elm, beech, aspen, birch (Caucasus and eastern Siberia), lime, pear, rowan, bird cherry, willow, prickwood, hazel (mainly catkins), blackberry, raspberry, jasmine, Guelder rose, buckthorn, currant, honey-suckle, ivy, mistletoe, and many other species at different places. For example, in the Far East deer consume well, among others, Amur philodendron, Manchurian aralia, and lespedeza; in the Caucasus yew (upper portions of small trees); in Crimea smoke tree (*Rhus cotinus*) and others. When other food is not abundantly available in winter, pine shoots with needles and even juniper are eaten in significant quantities (Belovezh Forest, Mordov, Voronezh, and Crimean preserve). In the Caucasus green leaves and stalks of ephemerals represent a main winter food item; ivy leaves are also very important in winter in Trans-Caucasus. In spring flowers of Dahurian rhododendron are also eaten well (Gassovskii, 1927). Fir, spruce, and larch are eaten rarely and that too only when there is a paucity of food in winter. Excessive consumption of pine needles, a food deer may be forced to eat, can disturb the functioning of the gastrointestinal tract and cause poisoning among young animals (Mertts, 1953).[104] In Belovezh Forest instances of death of deer due to excessive intake of spruce needles have been recorded (Wroblewski, 1927).

Depending on abundance, accessibility, preponderance, and chemical composition (which has never been studied), the importance of a particular species of tree as deer food can vary considerably. For example, the branches, shoots, and dry leaves of oak serve as the major winter food of deer in Crimean preserve; oak in this region is consumed more often than any other tree or shrub (Yanushko, 1957). In Belovezh Forest oak occupies only fifth place after other tree species, while in Voronezh preserve it drops to tenth place (Kaznevskii, 1958).

In Bashkir preserve lime and juniper are fairly common but deer do not consume them; yet in Belovezh Forest lime is eaten quite
150 often and even juniper is consumed (P.F. Kaznevskii). In places
where winter is relatively mild and thaws frequent (southwestern USSR, Crimea, the Caucasus, and Primor'e region) not only branches, shoots, etc., but also soft bark are eaten; in general, however, the importance of bark is particularly great in transitional

---

[104] In the snowy winter of 1955 to 1956 deer in Voronezh preserve consumed pine needles in large quantities (Kaznevskii, 1958).

seasons, i.e., in autumn and later in spring. In rare cases deer also eat bark of coniferous trees, for example pine and more rarely spruce, along with bark of deciduous trees. Pine bark is eaten in small quantities in summer when deer also gnaw at the upper root portions of spruce (Latvia; Kalnin'sh, 1950).

In the latter half of summer and in autumn deer avidly consume fruits of many fruit-bearing trees; Damson plum, pear, apple, and others; they also consume the succulent fruits of some shrubs as well as berries. Acorns and beechnuts are particularly important in the Caucasus. Deer utilize acorns as food not only in autumn but also in winter; when the snow is not more than 25 to 30 cm thick, it is not difficult to dig them up with muzzle and hooves. They also eat hazel nut, chestnut, pine nuts (Baikov, 1915; Yanushevich and Blagoveshchenskii, 1952), lime, etc., but these food sources, compared to acorns and beechnuts, are not very important.

Deer consume many types of mushrooms including white and peppered, russula, honey agaric, etc. In winter, especially in snowy periods, deer often consume epiphytic lichens (*Usnea barbata, Parmelia,* and others). Red deer have been observed time and again digging under snow for lichens (down to 20 to 25 cm) just as reindeer do when there is a food shortage. Lichens dug up include *Cladonia alpestris, C. rangiferina, C. sylvatica, Cetraria islandica,* and others (Belovezh Forest, Voronezh, Mordov, Azov-Sivash, and Crimean preserves, and northwestern Trans-Baikal). This phenomenon underscores the extraordinary ecological adaptabilty of red deer. It has also been recorded that deer consume both fresh-water (filamentous) and marine algae washed ashore. The consumption of marine algae and other sea products washed up on coasts (crabs, fish, etc.) is evidently motivated by the animal's need to meet mineral and possibly protein requirements. The volume of food in the stomach of a deer reaches 30 liters or more (April; Mertts, 1954).

Over much of the range deer visit waterlogged and sometimes dry salt licks. In winter deer clamber onto ice crusts on rivers and lick ice, which is rich in mineral matter because formed from montane water (Kirilov, 1902; Kaplanov, 1948; Okhotina, 1957; and others). When a shortage of fresh water occurs, deer drink sea water, taking it in small gulps (Azov-Sivash preserve; V.A. Mattskov; and others). Drinking sea water has also been observed in Primor'e region (Kaplanov, 1948) and probably follows the same pattern as in salt licks. Bukhara deer lick salt outcrops (Flerov, 1952). Visits to salt licks are most frequent in spring and the first half of summer; such visits also occur during the period of estrus but are far less frequent.

Home range. Fairly fixed home ranges are quite characteristic in those sections of the range where the population lives year-round in the same place, without resorting to major seasonal migrations (Graf, 1956). In the Soviet Union this is observed, for example, in Voronezh preserve, where deer are relatively settled and territorial behavior is relatively well manifested. A complete change of biotope and significant changes in herd characteristics are typical of the transitional season; both are highly constant throughout the rest of the year. Adult females with fawns or at the head of a herd often shift home range in summer (Graf, 1956); adult males typically relocate with harems in the period of rut (Mertts, 1953; Graf, 1956).

Mention is made in literature that deer mark the boundaries of their territory by various methods ("loners" and also adults acting as leaders of herds). Such territorial demarcations include "scratches" at definite places on the bark of trees and odoriferous deposits, due to rubbing up against trees, urination, etc. Animals not belonging to a given herd and entering a previously claimed territory are usually driven away (Graf, 1956). Territories are generally separated by
151 neutral zones, but if the population density is high, as in Crimean preserve, the boundaries overlap (territory of loners and herds) (P.A. Yanushko).[105] In the course of a day deer use only a part of the territory. In visiting salt licks they go beyond the boundaries of their territories, sometimes up to 4 or 5 km; salt lick zones are therefore neutral.

The size of the home range depends on the availability of food in the area and the population density. In winter, when places suitable for supporting deer life are usually smaller than in summer, animals congregate in a limited territory.[106] Size is minimal in the latter half of winter, especially if it is snowy. In summer in Voronezh preserve a small herd of deer is confined to a segment of 300 to 400 hectares, while in winter even a herd of 10 animals moves within a territory of not more than 200 hectares. With heavy snows a deer herd often will not wander more than a kilometer. In the period of fattening, beds are set up at intervals of 150 to 200 m (Mertts, 1953 and 1957; and others). Maral acclimatized in Mordov preserve traversed 2,200 to

---

[105] Black-tailed mule deer (*Odocoileus hemionus*) (California, USA) in such an event vigorously defend only the central part of their home range (Dasman et al., 1956).

[106] In Altai (Dmitriev, 1938), Caucasian (Zharkov, 1940), and Voronezh (Mertts, 1953) preserves the total area of the main wintering sites of deer constitutes only 30 to 40% of the area of their summer habitats. In some wintering areas deer density reaches 40 to 50 animals per 1,000 hectares (Caucasian preserve; Zharkov, 1940). In Voronezh preserve, toward the end of the snowy winter of 1955 to 1956 it even exceeded 60 (P.F. Kaznevskii), thinning down by five to eight times in summer.

2,400 m every day on a loose snow cover of 40 to 55 cm depth in February–March (F.D. Shaposhnikov). In Bashkir preserve, where maral are also acclimatized, their daily wandering in different seasons varies from 200 to 300 m (in winter when feeding on hay) to 4 to 5 km. In summer some females, from fawning to estrus, live in a sector of 90 to 140 hectares, traversing daily not more than 500 to 700 m (Kaznevskii, 1956; and others). In Crimean preserve, where deer density is exceptionally high (see above) and trees and shrubs have been highly denuded, a home range is limited to 40 to 140 hectares, on the average 70 hectares, and daily wanderings to 4 to 5 km, on the average 3.5 km [*sic*] (Yanushko, 1957; and others).

Judging from the few observations made in the Altai, western Sayan, and central Sikhote-Alin, where winter is extremely snowy, one may assume that deer at that time of year are confined to even more restricted areas than in the European part of the USSR. In the event of ice crusts the animals cannot go beyond two to three hectares for a few days at a stretch. In Caucasian preserve in the mid-1930's it has been stated that the home range of a male in rut with a harem of females usually did not exceed 400 to 500 hectares (Nasimovich, 1941).

Daily activity and behavior. In hot weather in summer deer stop grazing by 8:00 or 9:00 a.m. (as soon as the dew dries); grazing is resumed around evening and extends, with intervals, into the night. In cloudy weather and light rain, especially when the animals are not frightened, grazing deer can be seen at all hours.[107] For precisely the same reason, high in the mountains where it is much cooler, many deer graze even during daylight hours, as observed in Caucasian preserve.

In summer relatively open and windy areas (ridge crests, openings in woods, slightly sprouted burned-over forest sections, river shoals, lake banks, etc.) as also dense, well-shaded thickets of tall grass, shrubs, etc. serve as beds and sites for cud chewing, depending on the time of day, air temperature, abundance of various blood-sucking insects, etc. In Caucasian preserve female deer quite often lie in such tall grass that they are completely hidden; males do not make beds in such places. In large burned-over forest sections deer go to a lake (alpine segment of western Caucasus) or a river (the Sayans) and sometimes lie on snowfields when midges are prolific. To save
152 themselves from mosquitoes and gadflies deer of Azov-Sivash preserve descend into the water of bays and lie with only their heads above the water (M.D. Shpigov).

---

[107] They usually do not graze during heavy rains.

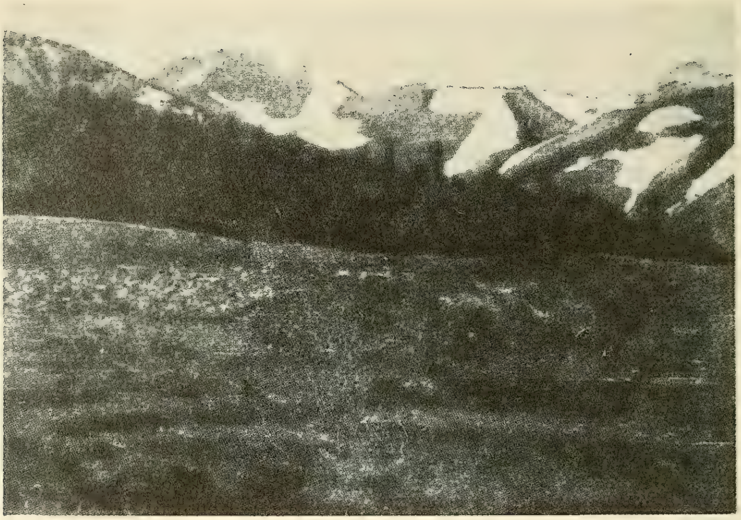


Fig. 50. Summer habitat of deer in the Caucasus. Subalpine glade on Abago mountain. July, 1946. Caucasian preserve. Photograph by I.V. Zharkov.

Bukhara deer graze mainly at night in summer, usually far away from rivers (where mosquitoes are prolific) at the border of deserts; during the day they rest in forests (not avoiding saline sections); when there is a rise in water level they lie directly in the water (Flerov, 1935). When threatened by mosquitoes, deer of Darganatinsk tugais quite often enter neighboring desert sections at night. Night grazing in the tugais is interspersed with periods of rest (Klyushkin, 1949). Deer visit salt licks and waterholes mainly during hours of darkness, but in Caucasian preserve they are often seen in salt licks during the day as well.

In winter, especially if there is a food shortage, deer spend most of the day feeding and, if not threatened, the activity rhythm depends not so much on the time of day as the weather conditions. During frosts, without wind, deer are generally more active than in mild weather; they try to protect themselves from the wind in ravines, more frequently in shrubs, among dense coniferous plantations and sometimes in caves (Crimea). They remain in their beds during intense snowfall. In winter sunny slopes with open vistas are a favorite place for beds in mountains. In valley sections where the wind blows rather continuously deer usually do not make beds; quiet places are invariably preferred (Kaplanov, 1948).

The weight load on the hooves of deer is considerable; in adult animals it is 450 g per cm^2 (Voronezh preserve; Mertts, 1957); in

Crimea, evidently, it is much more (Yanushko, 1955). Thus with an increase in height of snow cover deer movement becomes increasingly difficult. In order to ease their movement on snow deer utilize their earlier tracks and walk under dense crowns of coniferous plantations. In addition they reduce their mobility and feed intensely at a single place at such times. The critical height of snow cover for adult Altai maral is about 70 cm; the corresponding value for most other forms of red deer is 50 to 60 cm. In their search for items of food such as plant remains, acorns, beechnuts, etc. deer dig up the snow with their muzzle (if the snow is loose) and hooves, but only as long as the snow cover is less than 25 to 30 cm deep.

153 Deer move quite fast and can cover 4 to 5 km in an hour. Frightened, they immediately gallop but rarely trot; the span of a jump can exceed 6 m. Deer are excellent swimmers and instances are known of their swimming through turbulent (Terek and Pyandzha) and broad (Lena) Rivers or, to save themselves from wolves, even swimming several kilometers into the sea (Abramov, 1954).

Olfactory and auditory senses are well developed in deer; vision is evidently equally good but the animals are not so dependent on it. While feeding, the head is usually held high in the air. Instances are known of a sleeping deer (bedded or standing) walking off almost instantly on being awakened.

In regions where winter is relatively snowy the gregarious tendency is more pronounced in the cold period of the year than at any other time. Not only are mixed herds formed (more common in winter but the number of adult males in them is almost invariably small), but also herds consisting exclusively of males or females with young (herds of the second type contain a larger number of animals). In winter mixed herds are often formed from autumn harems with fawns and juveniles of ages 1.5 to 2.5 years, which had separated in the period of rut.

In spring, before breeding, mixed herds as well as those comprising adult females and young break up. Many small herds are then formed from the "large family" of an adult female (playing the role of a leader) and the offspring raised over several years.

Herd size depends mainly on overall deer population, amount of food in the region, etc. The usual herd size is three to six animals, rarely more (in the western Caucasus from the end of the nineteenth to early twentieth century deer herds consisting of up to 70 animals were recorded; Dinnik, 1910). Even in Crimean preserve, which abounds in deer, about 60% of the entire population is contained in herds of 4 to 10 animals each, with 30% in smaller herds and only 10% in larger ones (Yanushko, 1957).

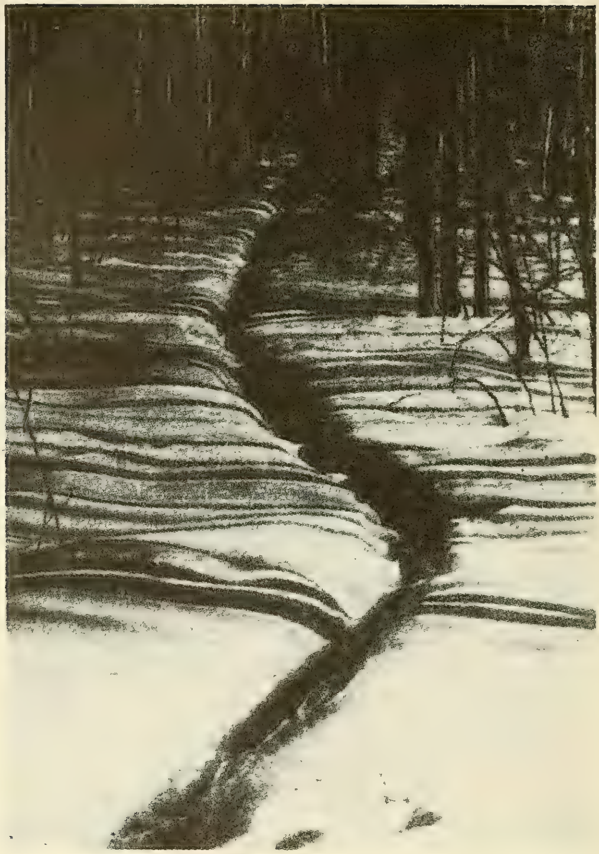


Fig. 51. Deer track. Voronezh preserve. March, 1958. Photograph by P.F. Kaznevskii.

Seasonal migrations and transgressions. Depending on the nature of biotopes, food availability, distribution and thickness of snow cover, and other factors, deer winter in the same locality where they lived in summer, only changing over from one type of habitat to another (Belovezh Forest and Voronezh preserve). Sometimes they undertake more extensive migrations, especially in montane regions (Carpathians, Crimea, the Caucasus, southern Siberian mountains, and Sikhote-Alin). The maximum number of deer congregate for
154 wintering in regions where the snow cover does not exceed 40 to 60 cm, but adult males often winter in mountains where the snow cover is 100 cm or even thicker, provided there is abundant twiggy food (western Caucasus and Altai). Wintering in such places is facilitated

by the absence of wolves, which congregate in less snowy regions (Derevyanko and Zharkov, 1953). Since females, fawns, and juveniles choose wintering places where the snow cover does not exceed 40 cm, places of mass wintering of females and adult males often do not coincide; the latter usually locate at higher altitudes.

In the mountains, in addition to downward vertical migrations in autumn, winter migrations to wind-protected, leeward slopes occur in less snowy mountain belts (range of vertical migrations may go up to 1,000 to 1,500 m). Such slopes provide a more favorable situation with relation to snow than excessively snowy windward slopes (Altai, the Sayans, Kuznetsk Alatau and Barguzinsk ranges). Having gathered in such leeward sites for wintering, the animals often cross several parallel ranges for feeding. The distance covered during wanderings in some cases ranges from 50 to 140 km (Nasimovich, 1955).

Migration to wintering sites usually occurs gradually and extends for a period of 1.5 to 2.0 months and sometimes even longer. More often, movement commences in the period of rut or immediately after it (rarely before), i.e., from October, and ends in November (more rarely in December–January). The first to reach the

154 Fig. 52. Two-year-old female maral. Mouth of Ad-Kicha River near Lake Telets. Altai preserve. End of February, 1951. Photograh by F.D. Shaposhnikov.

wintering sites are females with young. Heavy snowfalls accompanied by cooling and seasonal changes in the landscape serve most often as a signal for the commencement of mass migrations. Under these conditions, when the snow thickness exceeds 20 cm, it becomes difficult for deer to dig up plant food from under the snow.

In the Caucasus and Sikhote-Alin in the second half of winter, when snow is heavy, secondary migrations of deer occur down the 155 slopes into less snowy sections (Nasimovich, 1939; Kaplanov, 1948). In the event of formation of ice crusts deer congregate along well-shaded slopes in fir, spruce, and cedar forests.

The return to summer habitats commences in the period of intense snow thawing and is over in May or early June. The migratory paths of deer in many regions are fixed and coincide sometimes with those of elk and roe deer.

Summer dispersal and migration of deer depend greatly on the availability of food, shelters in the locality, and absence of blood-sucking insects. For example, in the Sikhote-Alin mountains with the appearance of midges (June) many Manchurian wapiti, especially the males, go high into the mountains and congregate there in deciduous, burned-over forest zones near glades, where blood-sucking flies are few because of the openness of the expanse and stronger winds. In the latter half of summer, with the onset of intense heat and the mass appearance of gadflies, these deer desert the open mountains and congregate in cool, wet, and shaded places (bottomland deciduous forests, river drainages, alder thickets, and boreal forests) where they suffer less from gadflies and heat (Kaplanov, 1948).

The small population of Bukhara deer performs only local migrations. In the Vakhsh basin the manifestation of such migrations is extremely poor; in spring and summer when the water level rises deer only desert to drier islands, continuing to wander along submerged areas (Flerov, 1935). Migrations caused by floods are seen in Darganatinsk tugais. In other cases migrations of deer are mostly related to agricultural and other activities of man. On being constantly exposed to threats deer often migrate from one set of tugais to another or even move off into the desert for some time (Klyushkin, 1949). In the Syr-Darya basin Bukhara deer have now been almost exterminated. Here they formerly spent much of the summer in saxaul thickets. In August, due to scarcity of water in Kyzylkum, deer came close to the rivers and were confined to the tugai zone; in November, at the commencement of snowfall, they again went into the desert (Bobrinskii, 1933).

Instances of reappearance of deer in regions from where they had disappeared long ago are a frequent phenomenon in many parts of their geographic range. Such instances have been recorded time and again in the northern and eastern Pri-Caspian (Bazhanov, 1945), northern Caucasus, [108] and other places. In Bashkir preserve, where maral had acclimatized, their appearance in new habitats usually occurred in the latter half of winter and was associated with food scarcity at that time of year, leading to wanderings. In snowy winters (1941–1942, 1942–1943, 1947–1948, and 1949–1950) intrusions into new habitats have assumed mass dimensions; some of the animals settled down in new places and did not return to old habitats in spring. The range thereby enlarged gradually and maral dispersed mainly along river watersheds covered with sparse pine forests and later even occupied bottomland areas (P.F. Kaznevskii).

In the winter of 1953 to 1954, during snowstorms on Biryuchii Island (Azov-Sivash preserve), some deer reached Arabatsk Strelka (Crimea), covering a distance of up to 30 km on ice (Ishunin, 1956).

Reproduction. Deer come into rut in autumn. It is manifested in some males externally by bellowing [bugling], initially not so loudly and for only a very short period, by the end of August or early September (in some cases from August 20 to 25).[109] During the second half of September bellowing intensifies both in number of participants and loudness and can be heard over a distance of several kilometers. In most cases mass bellowing occurs in the second half of September but sometimes in October also. In the latter half of October bellowing ceases, but some stray males in some years can be heard in November and, in exceptional cases, even in December–January.

During the period of maximum bellowing deer commence with broken and hoarse sounds resembling heavy breathing ("ahh-ahh-ahh") followed by a low, powerful, and prolonged mooing ("ee-ah-ooo-ooo-oooo") in which the last syllable in males of up to 2.5 years of age resembles a howl. Among Voronezh, Crimean, Caucasian, and Altai deer the style of bellowing is generally similar but the pitch in some cases higher than in others. Manchurian wapiti and Bukhara deer are characterized by extremely low and hoarse bellowing.

The bellowing period generally varies from one to two months; there are, however, extreme variations in different years in duration, harmony, and intensity of bellowing. Weather, feeding, and other seasonal conditions exert great influence on the nature of bellowing and rut. Following the extremely snowy winter of 1944 to 1945 Manchurian wapiti in Sudzukhin preserve bellowed very little (G.F. Bromlei). In 1908 deer of western Caucasus suffered from foot-and-mouth disease and did not bellow at all that autumn (Dinnik, 1909). Even in normal years part of the adult male deer population (usually not less than 20 to 30%; Zharkov, 1952; and others) will not bellow. If the sex ratio in a population tends to approach 1:1, competition for females intensifies and so, too, does bellowing. In populations with a significant predominance of females bellowing is usually less intense (Mertts, 1954; and others).

---

[108] For example, in 1956 a small herd of deer was sighted in an "island" of forest in the plains near Crimea station in northwest Krasnodar region, 50 to 60 km away from the nearest mountain (A.V. Vinogradov).

[109] In an extremely rare case the weak bellowing of a lone deer was heard even on August 15 and 16 (Sikhote-Alin and Crimea).

Commencement of bellowing and the subsequent course of rut are largely predetermined by phenological conditions: coloration of the landscape, onset of frosts, and so on (Sablina, 1955; and others). A perceptible drop in air temperature around the time bellowing should commence activates the males. If cooling is accompanied by inclement weather, prolonged rains, etc. after deer have been bellowing for some time, its intensity drops or it ceases altogether. If the autumn season is rainy throughout, bellowing is dull, unenthusiastic, and extended for a longer than usual period (Nasimovich, 1936 and 1941; Kaplanov, 1948; Yanushko, 1947; and others). Deer bellow mostly in the evening and morning but at the peak of rut throughout most of the night, especially on moonlit nights (Nasimovich, 1941).

In Crimea mass bellowing of deer usually occurs from September 21 to 26 (Yanushko, 1957). In Caucasian preserve mass bellowing has been recorded in various years from September 20 through October 5 (Nasimovich, 1941). A sizable number of deer commence bellowing earlier, from September 15, in the Laba basin where the mountains are high and the climate more continental. In the Beloe basin full-throated bellowing usually commences a few days later. In the Golovinka basin, on the southern slope of the Great Caucasus range, it commences from September 25 only (Zharkov, 1952).[110] In Zakatal'sk and Lagoda preserves, where the climate is much milder than in Caucasian preserve, mass bellowing of deer usually occurs at the fag end of September and in the first ten days of October (I.F. Popkova and G.P. Enukidze).

In Altai preserve peak bellowing among maral has been recorded from September 16 to 17 through 22 to 24, lasting usually for five to seven days (Dmitriev, 1938). In the middle part of Sikhote-Alin, mass bellowing of deer is most often heard from September 20 through 25, and in southern Primor'e region from September 25 through October 1 (Abramov, 1954).

---

[110] According to Kotovshchikova (1936) Crimean deer located in lower montane altitudes begin bellowing earlier.

References to periods of rut among Bukhara deer are contradictory. According to Flerov (1935 and 1952), Klyushkin (1949), and other researchers bellowing commences mid-September and sometimes even later (in Darganatinsk tugais often only from early October) and ceases in the latter half of October or even early November. Deer commenced bellowing in Tigrovaya Balka preserve from 1946 to 1950 from August 30 to September 6 and ended September 26 to October 5; mating was observed up to October 10 (Chernyshev, 1958). In Moscow Zoological Garden bellowing of Bukhara deer peaked in the first or second half of October—a delay of two or three weeks compared with maral (Tsalkin, 1944).

157 At the very commencement of bellowing many males are without females and remain alone, occupying a definite home range, sometimes the same one for two or more consecutive years (Caucasian preserve).[111] Sexually aroused males strike small trees with their horns, peel off the bark, and break branches and tops. By stamping with its hooves each male creates two or three "tochkami" (so-called by hunters)* of bald turf within its territory, sometimes saturating them with urine. Wallowing in mud in their bathing regions is also common among males in rut. In the second half of September many males (at the peak of rut not less than 50% or more) move with two or three females or sometimes more. In the mountains of the northwest Caucasus males with up to 10 females each have been sighted and in one instance in Crimean preserve a male with 19 females (including juveniles).[112] In maral farms males live with 4 to 15 or even up to 20 females (Zalesskii, 1930).

Males are capable of mating from the end of August (or slightly earlier) up to November and in some cases even later. In Crimean preserve individual males with traces of spermatogenesis have been caught in almost all months of the year. Mating is maximal from August to November, especially in September and October, after which it gradually declines (in April and May the tests are relatively inactive); sexual activity resumes in July or even earlier. The formation and development of follicles in the ovaries of adult females occurs throughout the year but Graafian follicles attain full maturity and ovulation occurs only in the period of estrus (Yanushko, 1957).

---

[111] The manner of bellowing of some males is so specific that they can easily be identified even in different years.

[112] Most juveniles (up to 1.5 years) live separately, away from adults, in the period of rut.

*Literally, "points"—Sci. Ed.

Mating usually takes place not earlier than mid-September, more often slightly later. In the middle part of Sikhote-Alin most Manchurian wapiti mate from mid-September to mid-October and in southern Primor'e region from September 25 through October 20 (Abramov, 1954). In Moscow Zoological Garden mating has been observed in the period of maximum bellowing and later, for a period of a month or more; most maral mate here from the end of September to early October, while most Bukhara deer mate later, in mid-October (Tsalkin, 1944). Mating is rapid and takes place while the animals are moving; a single female is usually covered several times.

There is no doubt that bellowing facilitates the location of males by females and at the same time exerts a stimulating influence on female estrus. During bellowing deer remain in places where their voice will carry long distances. The intensity of bellowing is inversely proportionate to harem size; males with large harems bellow less than males which, for some reason, are haremless. With the approach of a stronger competitor a male with a harem usually falls silent or even attempts to run away with his females (Kaplanov, 1948; Mertts, 1953; Abramov, 1954; and others). Deer judge the strength of a competitor not only from his external appearance but also from the nature of his bellow. In young males the bellow is very high pitched, while in virile animals it is very low and hoarse. There is no doubt, therefore, that weak bellowing is associated with fright and cannot be regarded as a "challenge to arms". Young males up to the age of 2.5 years hearing the call of a large male try to hide. In most regions fights over a female are not infrequent between adult males and may be violent at times, ending in the death of one or both rivals. Instances are known of antlers being broken or so entangled during a fight that the combatants could not separate themselves. Very often the approach of a rival is restricted to threats; the deer dash their antlers against trees but do not attack each other.

Some herds with harems are large, probably formed by the merger of two or more harems, and thus contain not one but two, three, or even more males. This phenomenon is relatively widely
158 prevalent in Crimean preserve where density of deer is very high and individual harems less isolated from each other than in other regions. Thus in Crimean preserve (1950 to 1954) 77% of all the

158 Fig. 53. Deer killed in a duel during the period of rut. Voronezh preserve. September 25, 1950. Photograph by P.A. Mertts.

harems sighted included one male, 18%, two males, and 5% three, four, or more males (Yanushko, 1957). Evidently larger herds with more than one male are not very stable and readily split into smaller ones with a single male in each.

Males bellowing actively (loners or those with small harems; Mertts, 1954; and others) eat little[113] and lose up to 30 to 40 kg or 20 to 25% of their summer weight during rut (Heptner and Tsalkin, 1947; Flerov, 1952). Judging from the results of mass shoots male deer in Crimean preserve lost during rut an average of 16% summer weight, but later recouped rapidly (Yanushko, 1957). At places where the climate is more severe, winter sets in early, and nourishing foods (for example, acorns) are not available every year, some males remain emaciated until winter. If in addition the winter is snowy and severe, mortality among adult males will be significantly higher than among females or even juveniles (Mertts, 1953 and 1957).

---

[113] In such deer the stomach contents might not exceed 0.2 liters (Mertts, 1954).

Among Crimean deer spermatogenesis commences from the age of 17 to 19 months, when males cannot yet be regarded as adults either in weight (75 to 123 kg), height at withers (96 to 118 cm), or structure of teeth and antlers. These deer do not participate in breeding and ordinarily do not bellow. Most males commence bellowing in their third year but even then do not usually participate in breeding because of competition from more powerful adult animals (Yanushko, 1957 and 1958). These data are based on a large amount of factual information and are evidently true for species of red deer as a whole. In maral nurseries instances are known of three-year-old males being mated with females who later fawned; usually males mate successfully only at the age of five or six years and rarely four (Zalesskii, 1930).

Among Crimean deer a few individual females come into heat in their second year when growth has not yet ceased;[114] most females, however, bear their first offspring only by the end of the third year; about 70% become pregnant in their third year during the period October through May (Yanushko, 1957 and 1958). In Latvia about 50% of all young females are usually impregnated in the third year, and by the end of that year bear their first fawn (Kalnin'sh, 1950). Similar data on periods of sexual maturity have been given for deer in Belovezh Forest (Sablina, 1955) and several other parts of the
159 range. According to the data of mass shoots of deer in Germany the number of pregnant females in their second year (total of 1,739 animals) in different regions varied from 0 to 63% or an average of 49% (Kröning and Vorreyer, 1957). Thus in the western sections of the range a significant percentage of females participate in mating and reproduce even in the second year. Possibly this should be considered the result of selection, fattening, and other measures adopted in game farms. In maral nurseries females become pregnant in the fourth or third year and rarely in the second.

Some adult females do not fawn every year (due to late fawning, sickness, age, etc.). The proportion of such females in the total number of mature females may reach 25% (Crimean preserve) or even 44% (Voronezh preserve) (Yanushko, 1957 and 1958). In populations of west European deer and American wapiti 20 to 25% are usually barren (Trippensee, 1948). Instances are known when females in maral farms fawned for four to six consecutive years; even then instances of barrenness were not uncommon (Zalesskii, 1930).

---

[114] Young females attract attention later than adults and hence some are impregnated late in autumn or even in winter (Mertts, 1954).

Gestation usually lasts 34 or 35 weeks but is probably somewhat longer in isolated cases. Delayed implantation is absent and the embryo is discernible even at the end of November (Caucasian preserve). Among most subspecies of red deer the majority of females fawn in the latter half of May (often only from the end of that month) or in the first half of June (more often up to June 10), but some individuals which have been impregnated much earlier, or on the contrary later, fawn even in the first half of May or at the end of June to early July.[115] Yet instances are known of isolated females attracting attention at an unusual time, mating, and bearing offspring very early, even by the end of March (Crimean preserve, 1947), or extremely late, in the latter half of November (Birobidzhan, 1925; Voronezh preserve, 1949). Significant deviations from normal fawning periods are frequent among maral. Bukhara deer fawn from the end of April through May inclusive (Flerov, 1935; Chernyshev, 1958; V.I. Chernyshev). In Moscow Zoological Garden fawning mainly takes place in June (Tsalkin, 1944).[116]

Females fawn in secluded spots, often in fern thickets or other vegetation along banks of rivers and springs. In an overwhelming majority of cases births are single. In Crimean preserve, of the 149 pregnant animals studied only one female with two embryos was found (Yanushko, 1957). In Azov-Sivash preserve from 1948 to 1953 twins were found only once in 71 births (G.I. Ishunin). In Altai maral nurseries roughly two sets of twins are born in every 100 recorded births (Zalesskii, 1930).

Growth, development, and molt. At birth a fawn* is weak and helpless. Attempts to stand are made in about half an hour after birth but usually are not successful in the first few hours; the animal has hardly stood before it falls down. At the age of three hours fawns of Bukhara deer can stand for some time and commence suckling (Tsalkin, 1944). For the first two or three days fawns lie down nearly all the time and stand up only to suckle. The mother moves a distance of 100 to 200 m to graze and feeds her young several times a day; at other times she usually stands apart to render detection of the fawn difficult by predators. From the fifth to the seventh day fawns begin to trail their mothers but are not stable on their legs even though they can run. At that age fawns suckle four to six times a day. Two-week-old fawns run and jump well; by July they are almost equal to adults in running. They begin grazing at the age of one month and soon after begin to chew the cud (Dobrzhanskii, 1928; Tsalkin, 1944; and others).

---

[115] In Azov-Sivash preserve over 10% females fawn in July, possibly because the deer population there is hybrid (G.I. Ishunin).

[116] Of 27 calvings among Bukhara deer in Moscow Zoological Garden, none was earlier than June 16 and some (37%) occurred in July (Tsalkin, 1944).

*Usually called "calf" in North America—Sci. Ed.

The young continue to suckle at least until early winter (there is often a gap in the period of estrus) and in some cases much longer. In maral farms pregnant females drive away the young from December onwards, while barren females allow the young to suckle until the next fawning and, should the fawn die, even longer. 160 Instances are known of females suckling newborn and one-year-old fawns simultaneously (Zalesskii, 1930; Tsalkin, 1944). Lactation before the birth of offspring is a frequent phenomenon among Latvian deer (Kalnin'sh, 1950). A few hundred deer were caught in Crimean preserve from 1951 to 1953. Among the females caught from July to September those lactating represented 74%, from October to December—69%, from January to February—41%, and from March to May—32% (Yanushko, 1958). Juveniles remain with the mother up to the age of 1.5 to 2.5 years; males usually separate at the age of 1.0 to 1.5 years; some young females, however, even after their first fawning rejoin their mothers.

Judging from the very few weighings of newborn deer from different parts of the range, their weight varies from 8 to 11 kg. The young grow very rapidly and put on weight for about six months; thereafter growth, especially in females, slows down and at the same time sexual dimorphism in size intensifies (P.A. Yanushko).[117] In maral nurseries three-month-old male maral weigh 46 to 67 kg (M 55); one-year-olds weigh 120 to 138 kg (M 130.6); two-year-olds 189 kg; three-year-olds 231 kg; four-year-olds 248 kg; five-year-olds 262 kg; six-year-olds 280 kg; and seven-year-olds and older 297 kg. By the sixth or seventh year weight increase ceases or becomes imperceptible.

Manchurian wapiti, as well as other subspecies of red deer, are inferior to maral in size; male adults weigh 170 to 250 kg and females 140 to 180 kg (Kaplanov, 1948). Judging from numerous weighings of Crimean deer, adult males in rare instances reach 269 kg and females 166 kg. On the average, however, the weight difference between adult males and females is about 50 kg (P.A. Yanushko).

Toward the end of the first year small bony prominences appear on the frontal bones of males. These prominences gradually grow into stumps which later serve as bases for antlers. The antlers them-

[117] According to Tsalkin (1944) sexual dimorphism in the size of maral is well manifested even by the third month.

selves begin to grow from 12 to 14 months; by the autumn of the second year growth ceases, ossification sets in, and the velvet is shed. These first antlers in an overwhelming majority of cases are devoid of tines and are variously called spikes or awls; these names are also applied to young with such antlers. The first antlers are usually shed in April, after which antlers with three or four tines begin to grow. In subsequent years the dimensions of antlers and their weight and number of tines increase (the tines do not increase in number until the animals are five or six years old or in the case of Bukhara deer four or five years old). Deer in the age group of 6 to 8 to 12 to 14 years have the best developed and heaviest antlers (in rare cases up to 16 and even 18 years of age), after which deterioration sets in with a reduction in size, number of tines, and weight. The weight of normally developed antlers of maral reaches 7 to 10 kg and in rare cases 18 to 20, or even 24 kg. Among Caucasian deer antlers weighing 7 to 8 kg are not a rarity, sometimes reach 10 to 11.5 kg, and exceptionally 14 to 18 kg. Adult Manchurian wapiti in Moscow Zoological Garden have antlers weighing 3.5 to 7.0 kg and Bukhara deer antlers weighing 3.5 to 5.5 kg (Turkin and Satunin, 1902; Dinnik, 1910; Tsalkin, 1945; Heptner and Tsalkin, 1947; Astanin, 1949; and others).

In most regions the majority of deer shed their antlers from the second half of March to early April. In the Baltic, Carpathians, Crimea, Azov-Sivash preserve, and the Caucasus, at least in some years, many deer shed their antlers even at the end of February (in Crimea some loners which have shed their antlers are sometimes observed from the end of January to early February; P.A. Yanushko). In Belovezh Forest shedding usually occurs only from the tenth of March. Maral in Bashkir and Altai preserves and Manchurian wapiti in the Far East shed their antlers only in the second half of March, often at the end of the month. References to periods of antler shedding among Bukhara deer are contradictory. Some stray deer, usually very young, shed their antlers later than virile stags and are
161 seen with old antlers until the end of April or early May, and in rare cases until the end of May or early June. In Moscow Zoological Garden delay in shedding of antlers by deer 2 to 4 years old compared to deer 5 to 13 years old, reaches almost 1.5 months. Shedding of antlers is also delayed in old deer (15 to 18 years), but not to the same extent as in young ones (Tsalkin, 1945). In years of severe winters antler shedding occurs later than usual (Bashkir preserve; Kirikov, 1952).

New antlers commence growing within a few days of old antler sloughing. New antlers are sheathed in a tender hairy skin, soft, and initially very sensitive not only to injury but also to mosquito bites (Przewalski, 1870). They are termed "velvet" antlers. In most deer antlers are fully formed by the end of June or the first half of July. After this they become ossified (July end to the first half of August) and the skin ("moss") is shed. This process is completed first in Crimean and Caucasian deer and later in maral and Manchurian wapiti (Tsalkin, 1945). For the first few days after the velvet is sloughed the antlers are light-colored but darken thereafter. References to periods of antler formation among Bukhara deer are contradictory. The ossification of antlers according to various researchers ceases by the end of July to mid-August and sometimes only at the end of September in the young. A 2.5-year-old male was caught in the Pyandzha in mid-August in which the antlers were still not completely formed and unossified (Flerov, 1935 and 1952).

In Moscow Zoological Garden the duration of growth of antlers among adult deer of various subspecies is similar regardless of antler size or structure. The process of antler formation requires 102 to 119 days, after which ossification continues for 30 to 40 days. The total duration of antler formation therefore requires 137 to 153 days. Skin is sloughed from antlers in one to three weeks. Antlers ossify three or four weeks before the commencement of rut (Tsalkin, 1945).

On the sides and back of young deer several rows of light-colored spots are visible, which gradually dull in the latter half of summer and disappear by autumn, after molt. Shedding of the juvenile coat in the first winter, essentially similar to the corresponding process in adults, terminates among maral of Moscow Zoological Garden in October, and among Bukhara deer in November (Tsalkin, 1944). In rare cases females continue to bear faint traces of spots even in the second year (Caucasian preserve). By February–March the hair has become intensely worn in adult deer, the beard brittle, and the fur lusterless and light-colored; some hair in the beard begins to fall in March. In much later stages of molt the underfur is usually shed, falling out in large tufts which cling to bushes when deer brush against them.[118] Deer molt most intensely from May to the first half of June, i.e., when relatively warmer weather sets in. The limbs and head are the first to be freed of winter hair, followed by the abdomen, thighs, sides, and back; the last to molt are the speculum, pelvis, and part of the neck (Tsalkin, 1946; and others). The summer beard begins to grow perceptibly from the end of April or in May.

In the southern parts of the range deer molt commences from the

---

[118] Among juveniles shedding of underfur is discontinuous and it does not fall out in large tufts (Tsalkin, 1946).

latter half of March (Azov-Sivash preserve, Crimea, and the Caucasus), but becomes perceptible usually only in April in the northern regions, which are climatically more severe (Mordov preserve and some regions of Siberia). Molt of Manchurian wapiti in the Far East (Kaplanov, 1948) and Bukhara deer in Central Asia commences in April (Flerov, 1935).[119] The commencement of molt and its course depend largely on the winter regime and the physical state of the animal. In Crimean preserve molt after a warm winter is apparent by the end of March (sometimes even mid-March), but after a very
162 cold winter evident only in April (in some years only from mid-April; P.A. Yanushko). The first completely molted deer in Crimea are observable in early May; nearly all deer sport a summer coat by the end of May, but in some years not until the first 10 days of June. In the more northern sections of the range and also where the mountains are significantly higher and the climate colder (Caucasus, Altai, and Sayan ranges), deer with large patches of winter hair can be seen even at the end of June or early July. In Moscow Zoological Garden, Caucasian and Bukhara deer molt by the end of June and maral and Manchurian wapiti by mid-July. The individual duration of molt extends over 2.5 to 3.5 months, being longest among maral (Tsalkin, 1946). The first to molt are adult males and barren females, followed by three-year-olds and females with fawns. The process of molt is far shorter in duration among juveniles than among adults.

The winter growth of beard commences at the end of July to early August but is only weakly discernible. By August the summer beard is partly shed and the growth of winter beard quite visible. The bright rusty summer coloration gradually changes to a rusty-gray and, as winter approaches, to grayish-brown. In September the summer hair, except on the head and limbs, is shed completely and the underfur commences to grow from the latter half of August, lengthening perceptibly. In the period of breeding deer sport transitional coats; the winter coat forms only in the latter half of October or early November but the lengthening of hair usually continues up to early December.

Among highly emaciated males in the postrut period beard growth and underfur formation are greatly delayed; in the event of early and intense cold weather this delay notably weakens such animals since considerable loss of body heat occurs (Mertts, 1953).

---

[119] The initial stages of molt in nature are difficult to perceive and most probably the reference to such a late commencement as April is erroneous. In Moscow Zoological Garden molt of maral, Manchurian wapiti, and Caucasian and Bukhara deer commences almost simultaneously in mid-March (Tsalkin, 1946).

Autumn molt generally occurs in a reverse sequence compared to spring molt. Initially the upper body parts, speculum, and more rarely sides, and later the underbody parts are freed of summer hair. The head and lower parts of limbs may not molt. Autumn molt is completed in a much shorter period than spring molt. Among adult maral in Moscow Zoological Garden molt lasts for 21 to 30 days and in juveniles for 15 to 23 days (Tsalkin, 1946).

In the colder parts of the range autumn molt terminates earlier than in warmer regions, by as much as two or three weeks. In Crimea the first completely molted deer are seen from mid-October, but animals with incomplete molting are evident right up to the middle of the following month (Yanushko, 1957).

In captivity deer may live for 20 years and in rare cases even 25 to 27 (Kirilov, 1902; and others).[120] In German game farms some deer live to the age of 25 to 30 years (Severtsov, 1940 and 1941; and others). Cases of deer in maral nurseries yielding up to 23 sets of antlers during their lifetime have been recorded (Cherkasov, 1884). In preserves, left to themselves, an overwhelming majority die at 12 to 14 years of age. Very old animals with totally worn out teeth are rarely encountered (Kaplanov, 1948; and others) and doomed to death in winter from hunger. The average life span of female deer in nature is unquestionably longer than that of males.

The last milk tooth in deer is invariably shed in their third year. Age-related changes in dentition, by which the approximate age of deer can be judged, have been detailed by Raesfeld (1911) and more recently by Beme (1957) for Crimean deer.

Enemies, diseases, parasites, mortality, competitors and population dynamics. Among the various causes of deer mortality over a vast stretch of their range, the most important are predators and severe snowy winters. Some diseases are equally important but their role in the population dynamics of deer has yet to be investigated.

163 In the region of the Voronezh preserve between 1933 and 1952 the number of recorded deer mortalities was 222 (excluding those killed by poachers). Of these, the cause of death was established for 208;[121] 54.3% died from emaciation during severe snowy winters,[122] 31.2% were killed by wolves, 13% died from fatal wounds inflicted in duels

---

[120] Kalnin'sh (1950) erroneously states that captive deer live up to 60 to 70 years.

[121] Among the unascertained causes of death, disease was undoubtedly an important factor.

[122] This category is identified easily, while that of destruction by predators often cannot be established; hence these figures should be taken as purely approximate.

during the period of rut, and 1.5% were drowned in rivers in spring. Among deaths caused by wolves (43 adult females, 20 female fawns, and only 2 adult males) over 90% occurred in winter months. Deer remains were found in winter in the stomachs and feces of wolves in 21.2% of all the samples analyzed; the corresponding figure for summer–autumn months was 5.3% (Mertts, 1953 and 1957).

In Belovezh Forest over 1,100 samples of the food of wolves were analyzed between 1946 and 1950; deer remains were detected in 7.2% (in maximum quantities in autumn and winter). In some years of severe snowy winters (for example, the winter of 1949 to 1950), the number of deaths of deer caused by wolves almost doubled (Gavrin and Donaurov, 1954). In Caucasian preserve no less than 60% of juvenile deer were once killed by wolves (Teplov, 1938).

In Altai preserve of the 107 deaths of deer registered between 1940 and 1951, no less than 63% were ascribed to the activity of various predators. As a matter of fact this number should probably be higher since an additional 9% mortality was attributed to deer falling from rocks in summer, often as a result of pursuit by predators. Of the 67 deer killed by predators, wolves were responsible for 45 and lynxes, wolverines, and bears for the rest (Dul'keit, 1956).

Adult deer are chased by packs of wolves or at least a pair; a lone wolf finds it difficult to cope with a deer, especially a stag. To protect themselves from attack deer lift the anterior part of the trunk and strike with the front hooves by extending them forward; males also make use of antlers in combat. Deer in montane regions attempt to rescue themselves from wolf attack by sheltering in rocks, in rapid river currents at relatively shallow spots, and when on the coast by swimming into the sea.

Compared with wolves the role of all other predators in destruction of deer is negligible. Apart from the wolf, deer are attacked most often by lynx, but a large number of such attacks are confined mainly to montane regions. Data on feeding by lynx in Caucasian preserve revealed deer remains in 8.3%[123] and in Belovezh Forest in 1.0% (Yurgenson, 1955). In Altai preserve of 56 instances of quarries chased by lynx 8 were maral. Family groups or pairs of lynx attack maral on snow; in one case they wounded an adult on snow crust (Dul'keit, 1953). In the eastern Altai and western Sayan, where winter is extremely snowy, maral attacks by wolverine are not rare (Kozhanchikov and Kozhanchikov, 1924; Dul'keit, 1953). Leopard and tiger are so few in number now that the damage inflicted by them on

---

[123] Attacks on wild ungulates by lynx have increased in recent years in Caucasian preserve (Kotov, 1958).

deer is quite insignificant; formerly deer attacks by them were a common phenomenon. In the Sikhote-Alin mountains among the quarries of tiger Manchurian wapiti used to occupy second place to wild boar (Kaplanov, 1948). Between 1946 and 1950 in Tigrovaya Balka preserve (Tadzhikistan) 19 Bukhara deer were killed by tigers; recently this deer has taken second place to wild boar in the food of local tigers (Sludskii, 1953). Brown bear,[124] yellow-throated marten, striped hyena, jungle cat, wildcat, jackal, and red wolf attack deer
164 sometimes, mainly the young, but on the whole the damage inflicted by them is negligible. In Caucasian preserve the death of a juvenile female deer was recorded as due to attack by two large predatory birds, evidently golden eagles (Nasimovich, 1936).

Deer suffer from foot-and-mouth disease, Siberian ulcers, cattle plague, infective abortion, necrobacillosis, necrotic stomatitis (agent *Spherophorus necrophorus*), pyroplasmosis, pasteurellosis, tuberculosis, leptospirosis (recorded in Slovakia), paratyphoid, and other diseases. Diseases in most cases were established not only in zoological gardens and maral nurseries, but also and usually under natural conditions. Epizootic foot-and-mouth disease has been detected time and again among deer of the northwest Caucasus (1908, 1911, and 1925), causing suffering and death among many animals. In those same years innumerable sick deer fell prey to wolves, being unable to run away quickly. Additionally, a high percentage of the survivors did not undergo rut. Epizootic Siberian ulcers have time and again caused heavy losses among maral and Manchurian wapiti in the Altai and eastern Siberia, both in maral nurseries and among wild animals (Turkin and Satunin, 1902; Novikov, 1937; and others). In the pre-Revolutionary period, Siberian ulcers wiped out maral farms in Trans-Bailkal (Lezhnin, 1922). This same disease has been detected in Belovezh Forest. In 1886 a large number of wild and domesticated Manchurian wapiti died of cattle plague in Trans-Baikal (Kirilov, 1902). In 1911 epizootic pasteurellosis raged among deer of Belovezh Forest causing multiple deaths (Vrublerskii, 1912).

Many instances of fatal diseases among deer remain undiagnosed (Novikov, 1937; Kolushev, 1955; and others). In western Europe rabies has been observed time and again among deer (Kovach, 1957; and others).

In Crimean preserve two deer mortalities have been established as due to theileriasis caused by the blood parasite *Theileria* (Rukhlyadev, 1948). The same parasite has also been detected in the blood of Bukhara deer (Chernyshev, 1958). The protozoan *Eimeria,* causing coccidiosis, has also been found in deer.

---

[124] In western Sayan, after wolverine, bear is considered the chief enemy of maral (Kozhanchikov and Kozhanchikov, 1924; Belousov, 1934). In this region wolves are few or altogether absent because of heavy snow.

On the whole, among deer of the *Cervus elaphus* group 65 species of helminths, including not less than 48 within the Soviet Union, have been identified (Belyaeva, 1958). In Crimean sanctuary alone 41 species of helminths have been reported for deer (Rukhlyadev, 1948; Kadenatsin, 1958). Among the most pathogenic and extensively prevalent helminths are *Dictyocaulus* and members of protostrongylids, causing grave pulmonary disorders (Boev, 1957). *Onchocerca bovis* infects leg joints, leading to lameness; this disease is not uncommon among deer of Caucasian preserve (D.P. Rukhlyadev). Infection of deer by liver flukes has been recorded in western Europe (Linke, 1957) as well as in Belovezh Forest. However, a lesser number of deer in the Forest have suffered from fascioliasis than European bison (Vrublevskii, 1927).

Parasitism of deer by the itch mite (*Sarcoptes scabei*) causes scabies (Kovach, 1957); in the Soviet Union this disease has been studied little. Deer are also parasitized by gadflies—nasopharyngeal gadfly (*Pharyngomia picta* and *Cephenomyia auribarbis*) (Grunin, 1957) and skin gadfly (*Hypoderma*). In May–June the larvae of *P. picta* were found in all 40 Manchurian wapiti examined in Sikhote-Alin preserve prior to 1950 (Kaplanov, 1948). Deer also suffer intensely from various blood-sucking arthropods, gadflies, mosquitoes, midges, *Lipoptena cervi,* mites (*Ixodes, Haemaphysalis, Dermacentor,* etc.), and other insects. A few hundred mites (*Haemaphysalis concinna* and *Ixodes ricinus*) have been found in some deer of Crimean preserve from April through July (Mel'nikova, 1953). Hair lice (*Trichodectes*), deer lice (*Pedicularis cervi*), and other lice also parasitize deer (Linke, 1957).

In regions with relatively severe and snowy winters the loss of deer is more in years when the snow cover significantly exceeds the average height and persists for a prolonged period, or in the second half of winter when an ice crust forms on its surface. In deep snow (65 to 70 cm or more) young deer break the crust with their hooves
165 and bog down in it without solid support under their legs. Even when the crust is so firm as to support them, adult deer often slip when running to save themselves from wolves, fall down, or cannot negotiate sharp turns (Mertts, 1957). Getting around becomes more complicated when the population of forest ungulates is high, resulting in a shortage of tree and shrub food. In this respect the history of deer of Voronezh preserve, is extremely interesting: initially, when the deer population was low, mostly juveniles suffered in snowy and

severe winters (for example, in the winter of 1939 to 1940) and later, as the herd grew, even adult animals, mostly males, died in greater numbers under similar winter conditions. Adult males, in the event of an acorn shortage, as happened in 1950, could not recoup after the period of rut and had to face the hard winter unprepared (Mertts, 1953 and 1957).

During the period 1933 to 1952 the winters of 1939 to 1942 and 1950 to 1952 (in all, five winters) proved particularly hazardous for deer of Voronezh preserve. In these winters death due to emaciation and other factors (excluding wolves) was established in 113 deer, of which 56.6% were juveniles, 41.6% adult males, and 1.8% adult females. Adult deer died mainly due to emaciation (instances of death became more frequent with the intensification of frosts), while juveniles died due to the consumption of large amounts of coarse food (Mertts, 1953 and 1957). Later, the deer population in the preserve rose, but during the extremely snowy and severe winter of 1955 to 1956 (snow height in some habitats exceeded a meter and the minimum temperature fell to −40°C), 177 of the 880 deer died.[125] Among deer which died in that winter due to emaciation and excessive cold, 42.5% were juveniles in their first year and 7.5% in their second year, 35% adult males, and 15% adult females. The wastage in the group of adult males comprised roughly 27% of the total population, among adult females 6%, and among the current year's brood 36% (Zharkov, 1957). The death of deer was maximum in sections where vegetation had been greatly damaged by cattle in the preceding summer (Kaznevskii, 1958). In Belovezh Forest starving deer died in winter due to consumption of spruce needles, which are unsuitable to them and cause nephritis and constipation (Wroblewski, 1927).

Mass deer mortality due to wolves, emaciation, and in part snow avalanches, was observed in the northwest Caucasus in the winters of 1910 to 1911 and 1931 to 1932 (Nasimovich, 1938 and 1939). During the most snowy winters in the last one-third of the nineteenth century deer in the Ingur and Tskhenis-Tskala were often totally destroyed (Kalinovskii, 1901). Instances of mass mortality of maral and Manchurian wapiti in snowy winters were a more rare phenomenon, but even so occurred in some winters, for example that of 1913 to 1914 (mountains of southern Siberia and the Primor'e region; Solov'ev, 1921; Kaplanov, 1948; and others). In the Far East a large number of Manchurian wapiti died due to hunters, predators, and other reasons in the winter of 1865 to 1866 (Przewalski, 1867)

[125] Over 100 more deer died outside the preserve area.

and in the snowy winter of 1935 to 1936 (Kaplanov, 1948). Mortality among maral and Manchurian wapiti due to shortage of adequate food was also noted in the winter of 1940 to 1941 (Sayans and Barguzinsk preserves; Nasimovich, 1955). In Altai preserve mortality of maral due to snow avalanches has been recorded (Dul'keit, 1955) and in the Primor'e region of Manchurian wapiti due to wolves when massive slippery crusts formed on rivers (Okhotina, 1957).

The winter of 1953 to 1954 was severe in the southern Ukraine and accompanied by the formation of ice crusts and deep snow (up to 55 cm). In this year, of the 133 deer in Azov-Sivash preserve, 46 died due to emaciation and excessive cold; of these 42.4% were adult males, 36.2% juveniles, and 21.4% adult females (Ishunin, 1956). Here, too, male mortality was considerably higher than that of 166 females. In 1949 unparalleled floods in the Amu-Darya and intense flooding in Darganatinsk tugais claimed 50 of about 100 Bukhara deer (Klyushkin, 1954).

While on the subject of deer mortality mention should be made of the high mortality rate among adult males in the period of rut. In Voronezh preserve over a period of 20 years 27 cases of death of males as a result of duels in the period of rut have been recorded, representing 13% of all deaths for which reasons have been established (Mertts, 1957). The high rate of mortality among adult males in severe winters as a result of emaciation in the period of rut should not be overlooked. In Crimean preserve 33 cases of death of deer were established for the period 1945 to 1950. Of these, deaths due to various traumas, including those inflicted during duels in the period of rut, accounted for 30% (Yanushko, 1958). Hence, even in those deer populations where their number is uncontrolled, among adult animals there is a significant preponderance of females even though at birth the ratio of the sexes is close to 1:1 (Yanushko, 1958; Kröning and Vorreyer, 1957).

Based on data of encounters between adult male and female deer, obviously not very accurate (females usually remain in large groups and thus draw immediate attention), the following ratio of males to females emerges in different regions:

Preserve	Years	♂ : ♀	Reference
Belovezh Forest	1945–1949	1 : 1.2	Sablina, 1955
Voronezh	1941–1953	1 : 1.6	Mertts, 1953
Voronezh	1955	1 : 1.8	Zharkov, 1957
Crimea	1945–1950	1 : 1.6	Yanushko, 1958
Caucasus	1927–1935	1 : 1.7–4.0	Nasimovich, 1936

Preserve	Years	♂ : ♀	Reference
Borzhom	up to 1946	1 : 2.5	Z.S. Ekvtimishvili
Zakatal'sk	1953	1 : 3.7	I.F. Popkova
Sikhote-Alin	1936–1941	1 : 3.0	Kaplanov, 1948

A large number of fawns die in the first few weeks or months after birth, either because fawning occurred early or the young fell victim to predators. Females also die when cold spells recur. Data on this subject are extremely scanty, however. In most regions juveniles in autumn or early winter populations comprise 11.0 to 13.4% (Nasimovich, 1941; Sablina, 1955; Zharkov, 1957; and others). In Crimean preserve, where wolves are absent, the maximum fawn mortality takes place at the age of three to four months; of the total number of young born in that period about 37% perish, mortality falling sharply in subsequent months (Yanushko, 1958). According to the calculations of Sablina (1955), based partly on data provided by Severtsov (1941), in Belovezh Forest fawn mortality in the first year of birth reaches 50% and drops to 40% in the second year (of those surviving at the end of the first year). Only 30% of the original year-class remains at the end of the second year.

In various preserves the annual growth of herds varies from 12.5 to 20.4%, more often 16 to 18% of the total number of animals. The highest growth rate of herds has been recorded in certain years in Crimean preserve. In the Voronezh, annual growth of the deer population dropped from the end of the 1940's to 12.5% (average for 4 years) from the former 17.4% (average for 13 years). Mertts (1953) explains this as due to dispersal of deer beyond the preserve into regions where they are greatly threatened by wolves, and also due to unfavorable conditions during one winter. The increase in density of population and consequent worsening of food sources could also perhaps have been contributory factors.

In taiga regions the most serious competitor for deer is elk; in Belovezh Forest, with mixed forests, the ratio of these two species is
167 more in favor of deer than elk, and the former is far more adaptable than all other ungulates with regard to food selection (Vroblevskii, 1912). The rapid multiplication of deer in Crimean preserve not only arrested the population rise of roe deer, but later even caused a reduction, perhaps partly due to migration of roe deer into the much lower mountain regions falling beyond the limits of the preserve. No less than 71 plant species, i.e., over 50% of all known deer food plants in that region, are common to both these species (Yanushko,

1957). In places where true and sika deer coexist the population of both is usually insignificant and hence data on competitive relations between them are scanty.

In Crimea beds of red and roe deer are often found in immediate proximity of each other; in winter Siberian roe deer are sometimes found among herds of Manchurian wapiti (Cherkasov, 1884). On encountering other ungulates at a salt lick deer do not descend into it until the departure of elk (izyubr' usually avoid salt licks patronized often by elk) and roe deer await the departure of [true] deer.

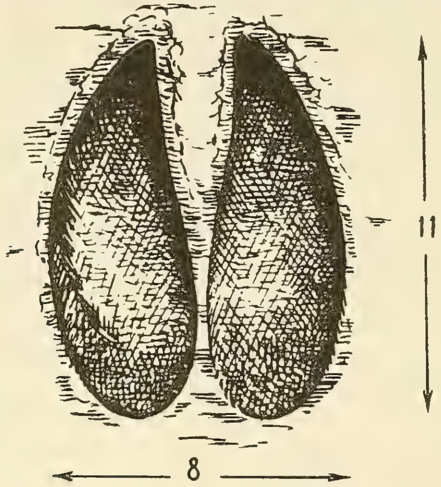
In Voronezh preserve deer visit in winter places where trees have been felled by beavers and feed on slender (up to 1.5 cm, aspen) terminal branches. In Azov-Sivash preserve crows collect in spring the wool of molting deer for building their nests, landing for this purpose directly on their backs (M.D. Shpigov).

In addition to economic and elemental factors, the population dynamics of deer in most parts of the range is also determined by man's influence on topography, which alters the original habitat. In the Ukraine the human factor over centuries has ultimately led to the disappearance of deer there. Bukhara deer have also suffered similar consequences as a result of destruction of tugais, and maral in Kirgizia have suffered from the cutting of spruce forests and reduction in their seedlings (D.P. Dement'ev, 1946).

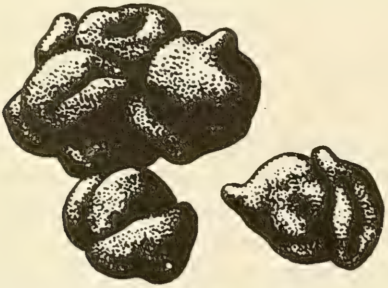
Field characteristics. In external appearance true deer are easily distinguished from roe deer and sika (see the field characteristics of these species). Females of true deer are without antlers and smaller in size than males.

During slow walking the distance between hoofprints is 50 to 70 cm, increasing during a gallop to 3 to 6 m. Hoofprints are oval and slightly elongated. Even on relatively stable soil not only the two medial large toes but also the two small lateral ones are usually imprinted (impressions of the latter fall in the rear). Deer hoofprints are similar to those of wild boar but the two medial toes of deer are less mobile and not as widely extensible as in wild boar; the impressions of the lateral toes of wild boar are more distinct and the hoofprints more elongated. The tracks of males are larger than those of females; even a three-year-old male makes a larger or at least equal-sized print as an old female. The hoofprint of a female is more oblong and narrow than that of a male. The shape of the hoofprint of a juvenile is similar to that of a female (young deer walk [rear] hoof on [front] hoof or even advance them slightly forward). The pace of the male is longer than that of the female; the clearance between the imprints of the right and left hooves is also greater in the male; the rear footprints of a male are more stunted. The urine patch touches the snow between the hoofprints of the fore and rear legs in the case of a male and close to the hoofprints of the rear legs in the case of a female.

168 Feces are in the form of oblong, dark cinnamon-colored pellets and form a cluster; the pellets are smaller than those of elk but larger than those of roe deer. In summer the pellets of an adult male measure 3.0 to 4.5 cm × 2.0 cm and of females 3.0 cm × 1.5 cm; the pellets of a male are generally more rounded than those of a female (the latter's is more elongated). In winter, when deer eat dry food, feces are more regular in form; in summer the pellets often fuse and their individuality is obliterated; in spring, during transition to grass feeding, feces initially take the form of large semifluid pancakes in which it is difficult to distinguish individual pellets.



167 Fig. 54. Hoofprint of male deer on soft soil in a forest (reduced). Voronezh preserve. October, 1950. Sketch by A.A. Nasimovich.



168 Fig. 55. Deer feces in spring. Crimean preserve April, 1952. Sketch by T.L. Savranskaya.

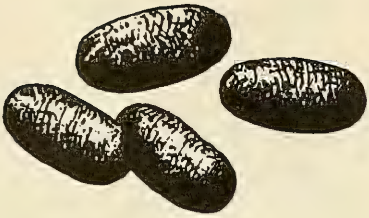


Fig. 56. Winter feces of female deer. Voronezh preserve. Sketch by T.L. Savranskaya.

The bed is oval in shape. In winter, while lying down, deer often scatter snow with their hooves, but sometimes lie down directly on it. Usually they lie with their head in the direction of the entrance. When snow is heavy the animals do not lie down at one place for long.

In winter deer groups form characteristic patches measuring up to 50 to 70 m in width at places of feeding. From the broken branches of deciduous trees and shrubs and the plucked tops of young pines these places are recognizable long after the deer have fattened. In winter gnawed bark reveals fairly deep furrows, narrower than those of elk (deer and elk scratch bark with their incisors); in summer, when bark can be easily peeled from trees, tooth marks are not left behind as the bark is removed in whole strips (Klyushin, 1949; Formozov, 1952).

Places of regular habitation of deer reveal well-beaten tracks, sometimes running for several kilometers and connecting pasturing meadows, salt licks, waterholes, shaded and sunny slopes of mountains, and so on. The presence of deer can also be judged from scratches made on trees by them while attempting to peel the skin from their antlers, from shrubs and small trees damaged and disturbed by the antlers (in such places, the turf and soil are stamped down by hooves and there is a distinct smell of urine), from clusters of dropped wool adhering to bushes, and so on.

Frightened deer emit a broken and not very loud "hau" (the cry of a frightened male roe deer is far louder). Females and young on registering danger emit short and fairly melodious sounds resembling squeaks; females sometimes make a low mooing sound. In nature, however, for most of the year, even in places where deer are extremely abundant, their voices are rarely heard. It is only in the period of rut that the bellowing of males can be heard over a long distance. (A.N.)

Economic Importance

Hunting of deer is strictly prohibited in most of their range because of their low population, but licensed hunting of adult males is permitted in Siberia and Georgia. Deer are killed almost exclusively by gun; the time of hunting is usually spring–summer (for velvet antlers) and autumn–winter; the best time in the latter period is the second half of November and the first half of December. In spring
169 and early summer deer are caught not so much for their meat (spring deer are often lean), as for obtaining young unossified antlers—the velvet antlers used for medicinal purposes (to enhance overall vitality and so on). Velvet antlers are of maximum value when they are not fully developed (this corresponds in different parts of the range roughly to May 15 to 25 through June 15 to 25). For obtaining velvet antlers deer are caught at salt licks, banks of water sources, well-frequented meadows, during transit, etc. Sometimes dogs are used to bring deer to bay; dogs are also used to track wounded animals. In winter deer are caught on the snow most often by stealth but sometimes by organizing a beat. Occasionally dogs are used and in this case deer run into rocky areas and stand there in sheltered spots; hunters take advantage of this habit.

Until recently hunting was widely practiced during the period of the rut; by locating the direction of bellowing the hunter approached the deer within gun range. To entice the stag to bellow more often, its bellow was imitated by cupping the hands in front of the mouth or a pipe made from stalks of cow parsnip, birch bark, etc. was used (hunting "with a pipe"). Many males during the period of rut are greatly emaciated; their meat takes on a bluish tinge and has an unpleasant taste. The products of such a hunt are of low value except for the hide, which at that time is of good quality. From the sportsman's point of view hunting "by bellowing" is one of the most interesting sports.

In pre-Revolutionary Russia a very large number of deer were caught by chasing them on ice crust or in deep snow. Deer were also caught in deep snow to replenish maral nurseries but a large number became exhausted in this process and died. At some places in Siberia such a catch resulted in greater loss of life and affected the population of deer more than ordinary hunting. Now the chasing of deer on ice crust and in deep snow is prohibited.

Also prohibited at present is the trapping of deer, extensively practiced before, mostly in Siberia and the Far East.[126] Special, long fences were built with pits dug at exits. Traps were also laid on deer trails and at salt licks.

---

[126] Nevertheless poachers even today sometimes use snares made of cable to catch deer.

In some southern regions of Siberia deer were formerly caught in the course of their autumn–winter migrations and near points of river crossings. This type of hunting is practiced very rarely nowadays.

For catching deer alive different types of traps are used (corrals, mobile traps with closing shutters, bait, etc.), but none is very effective. In Voronezh preserve chasing on snow was done to capture deer alive and nets sometimes employed.

By the end of the nineteenth century up to 25,000 or more deer had been caught in Siberia and the Far East (Solov'ev, 1922; and others). The main products of deer hunting are meat, hide, and velvet and ossified antlers; secondary products include tails, sex organs of males ("pyrki"), and fetuses removed from wombs ("lutai"). Secondary products are used in some regions of the USSR (Evenk, Nanaians, and others) as a stimulant during child-birth and for the preparation of drugs for different ailments (heart and sex disorders, malaria, and others).[127] The quality of deer meat is excellent in autumn before the onset of rut. At places where food is abundantly available and males are able to recoup at the end of rut, their meat as well as that of females is of high quality during the entire first half of winter. The meat yield, i.e., the body weight without head, hide, viscera, and hooves, constitutes 55 to 65% of the animal weight. A large maral (see section on growth and development) can yield up to 220 to 230 kg of meat (including up to 15 to 25 kg fat), a Manchurian wapiti up to 190 to 200 kg, a Voronezh deer rarely over 150 to 160 kg, and a Crimean deer generally less than 140 kg.

170 The high value of maral and Manchurian wapiti velvet antlers (less, however, than that of sika) led even in the nineteenth century to the founding of a special branch of animal husbandry, i.e., catching and raising of deer in paddocks. In the Altai raising maral commenced in the 30s of the nineteenth century on the Bukhtarma River. By the end of the century there were 200 nurseries established in the Altai, containing over 3,000 maral. In Trans-Baikal (along the Ingoda River) raising Manchurian wapiti commenced in 1843 and by the end of the nineteenth century there were 300 farms, containing over 1,000 wapiti (Turkin and Satunin, 1902). The extent of maral farming in the past in the Altai and the hunting of deer can also be judged from the fact that present-day Gorno-Altai Autonom-

---

[127] For more details, see Skalon et al., 1951 and Abramov, 1954.

ous Region prepared 6,600 maral hides and 1,116 pairs of velvet antlers in 1896 (Yukhnev, 1903).

Raising maral is now most extensively developed in the Altai. A valuable endocrine preparation, pantocrine, is prepared from the velvet antlers of maral and Manchurian wapiti (formerly the velvet antlers were mainly exported to China). European red deer have never been a source of velvet antlers.

In pre-Revolutionary years ossified antlers were exported to China (used in Tibetan medicine) and also to western Europe as decorative trophies. For the latter purpose antlers were removed along with part of the frontal bone. Even in the early twentieth century antler buyers from various cities, even Paris, assembled in the Krasnodar region. Antlers were used in making knife handles and other articles and for making glue by boiling them.

The quality of deer hide is best in the latter half of September to October. Hides are converted into tough chamois, and the hide with hair converted into warm fur coats, aviator boots, mittens, and other articles of apparel, covers for yurts (nomad tents), and edges for skis. Autumn hides, which are the toughest, are used for belts, breeches, bridles, etc.; spring hides, because of holes made by gadflies, are less valuable.

In the distant past attempts were made in Poland and Germany to use deer as draft animals (Turkin and Satunin, 1902).

Acclimatization of deer has long been attempted. In Belovezh Forest, where deer were extinct even by the middle of the nineteenth century, 18 deer were imported from Silesia in 1864. Later, from 1891 to 1902, about 300 deer were imported from Silesia, Bohemia, and Spala. During the 1870's and 1880's deer were imported from Poland or Germany into Ramon' and held captive until 1917 when they were set free. These deer represent the parent stock of the present-day Voronezh animals. In setting up the Borzhom game farm 83 deer had been imported by the end of the nineteenth century, mostly from Austria (58) and later from some regions of the Caucasus and Vil'nyus (in the latter case deer were not of local origin). The introduced deer interbred with native animals (Anon., 1891) and hence the current population of Borzhom deer is of hybrid origin. In pre-Revolutionary years deer were also released in the Baltic (imported from Belovezh Forest and western Europe), western Ukraine (imported from western Europe) and Askaniya-Nova (for the first time around 1894). In the latter region Crimean deer, Altai maral, and complex hybrids sharing the blood of several deer forms, including sika, can be seen today. In Latvia deer were reacclimatized not long before World War I (Kalnin'sh, 1950).

A large number of experiments for acclimatization of deer have been conducted in the last few decades. In 1928 five deer of hybrid origin were imported from Askaniya-Nova into the Biryuchii Islands (Black Sea). Nine more deer were added in 1946, also from Askaniya-Nova, and three in 1951 (V.A. Mattskov). In 1929 twenty-six hybrid deer from Askaniya-Nova were released in the region of Pecheneg village in Kharkov district. The deer released there have survived (in 1948 there were 16 animals, which rose to 60 before the Great Fatherland War [W.W. II]; N.V. Charlemagne). In the early 1950's ten deer were imported from Crimean preserve and twelve from Voronezh into Pechenezhsk game farm. Deer were also released in Gavrilov game farm of Kherson district, Ukraine, where by the end of the 1940's over fifty animals were counted. As a result of the construction of a water reservoir there almost no deer are seen now. In 1957 sixteen Voronezh deer were released in Korostansk forest farm of Zhitomir district, twenty-four (also from Voronezh preserve) in Vovchansk forest farm of Kharkov district, and sixteen from Crimean preserve introduced in Brovar region of Kiev district (A.P. Korneev).

After the First World War deer were introduced from Germany into Estonia and raised under conditions of partial confinement on the Abruk Islands (near Saaremaa Island) and northwest of Pyarnsk (Audr Forest). Only a few have survived in the latter region to date. In 1957 eight maral were introduced into Estonia and placed for the first time in confinement (E.V. Kumari). Also in 1957 thirty-seven deer were brought from Voronezh preserve into the Lithuanian Soviet Socialist Republic. In 1929 six European deer were brought into the territory of the present Molodechnensk district of the Belorussian Soviet Socialist Republic, then part of Poland. These deer formed the nucleus of a small population, surviving even at present in Ivenets and Volozhinsk regions. In 1949 they numbered fifty (Serzhanin, 1955). In 1957 forty-eight deer from Voronezh preserve were brought into Berezinsk beaver preserve (Nemansk basin) and thirty-six introduced into Krasnyi Les in 1948 (Krasnodar region). From 1940 to 1941 maral from Shebalinsk maral farm (Altai) were brought into Bashkir preserve and fifty-three set free in 1941 to 1942. They multiplied and later settled outside the limits of the preserve (Kaznevskii, 1954 and 1956; and others). In the same period Askaniya maral (complex hybrid) were acclimatized in Mordov preserve.

A few Caucasian deer were held for several years in Teberdin preserve. In 1953 four deer from that nursery were released in the Gonachkhir River region (deer in Teberda region became extinct even in the nineteenth century). In 1955 there were eleven deer (Inyakova, 1957).

In Zavidov game farm (north of Moscow), eight maral were released in 1938 but during the Great Fatherland War all were destroyed (Danilov, 1947). Recently, no less than seventy maral from Altai maral farms have been released in batches of six to thirteen animals in several game farms in Moscow, Kalininsk, and Yaroslav regions (Yurgenson, 1957; and others).

The main drawback in most cases of release of deer is the unacceptability of hybrid forms and release in the same region of deer belonging to different subspecies. In this context the preservation of Crimean deer, which are an entirely distinct subspecies, in pure form without admixture with other forms, should be safeguarded.[128]

One of the important problems of present-day game and sanctuary farming is to combine raising and protection of deer with afforestation. The experience of Belovezh Forest, Voronezh, and Crimean preserves, the Baltic republics, and western European game farms has shown that when deer population density is high, the animals adversely affect forest economy. Even though they only damage seedlings and shrubs severely in some winters, this renders the raising of mixed plantations by selecting deciduous seedlings and weeding out coniferous species difficult. A progressive increase in spruce and a decrease in proportion of deciduous species in the forest composition of Belovezh Forest was observed in the early twentieth century and associated with the then-high deer population (Vrublevskii, 1912; Kalnin'sh, 1950; Bannikov and Lebedova, 1956; Yanushko, 1957; and others).

In Voronezh preserve deer at places damage saplings of oak, pine, and other plants; in Belovezh Forest they damage saplings of ash, maple, oak, and other plants, while in Crimean preserve, damage is mostly confined to saplings of oak, beech, pine, maple, and some shrubs. In the Primor'e region Manchurian wapiti greatly damage philodendron and aralia. In places where efforts are made to combine forest growth and raising of deer the density of the latter should not exceed an average of 10 per 1,000 hectares of land; in sections of the range where food availability is less, this norm should evidently be reduced and in the south, where winter is not very severe, it should be raised slightly. At the time of implementing various forestry measures, shrubs and saplings should be preserved since they constitute the main food of deer in the winter. It should also be remembered that when the population density of deer goes up, the animals and their antlers are reduced in size, their fertility decreases, and many other undesirable consequences follow (Caesar, 1956; and others).

---

[128] A project for acclimatization of deer from other parts of the range in the mountain forests of Crimea was proposed in 1958.

In some instances forest deer, when relatively abundant, can threaten adjoining agricultural farms, kitchen gardens, melon fields, and haystacks left in forests. In the Crimea deer at places damage vineyards (they eat the fruit, break branches, and trample bushes) and visit fruit gardens. In the Amu-Darya tugais Bukhara deer visit farms where they avidly consume the herbage of mungo beans (*Phaseolus mungo*), damaging the plant along with flowers and green pods. Joughara [*Sorghum cernum*], sesame, lucerne [alfalfa], and muskmelon are also sometimes damaged by deer (Klyushkin, 1949). On the whole, however, these losses are rather insignificant and can easily be prevented by implementing appropriate measures for the control of deer populations. (A.N.)

172 Subfamily of Elk, or Telometacarpal Deer

Subfamily Odocoileinae Pocock, 1923

Deer of small, moderate, or large size.

Only distal extremities of metacarpals retained while proximal portions reduced to insignificant remnants, usually fused with cannon bone. Cuneiform either separate from naviculo-cuboid or fused with it.

Depression for preorbital gland on facial part of lacrimal, with a few exceptions (*Capreolus* and one species of *Pudu*), present and well developed. In several cases vomer divides choanae. Antlers invariably present; in one case (*Rangifer*) even females have antlers. Antlers extremely diverse in form and develop from simple, unbranched, short spike to very complex designs. Brow tine usually absent and later half of main beam often curves forward.

Tail short, of average length, or long. Bare patch at end of muzzle variable; sometimes very much reduced, absent, or very prominent. With a few exceptions (*Capreolus* and one species of *Pudu*), preorbital gland present and well developed. Toe pads highly developed and cover entire lower surface of hoof. Preputial portion of penis, with a few exceptions, fused with abdominal skin. In other features Odocoileinae do not differ from Cervinae.

These are forest, forest-steppe, and tundra animals.

Odocoileinae represent a typical group of deer of the New World, where they are widely scattered, very diverse, and represented

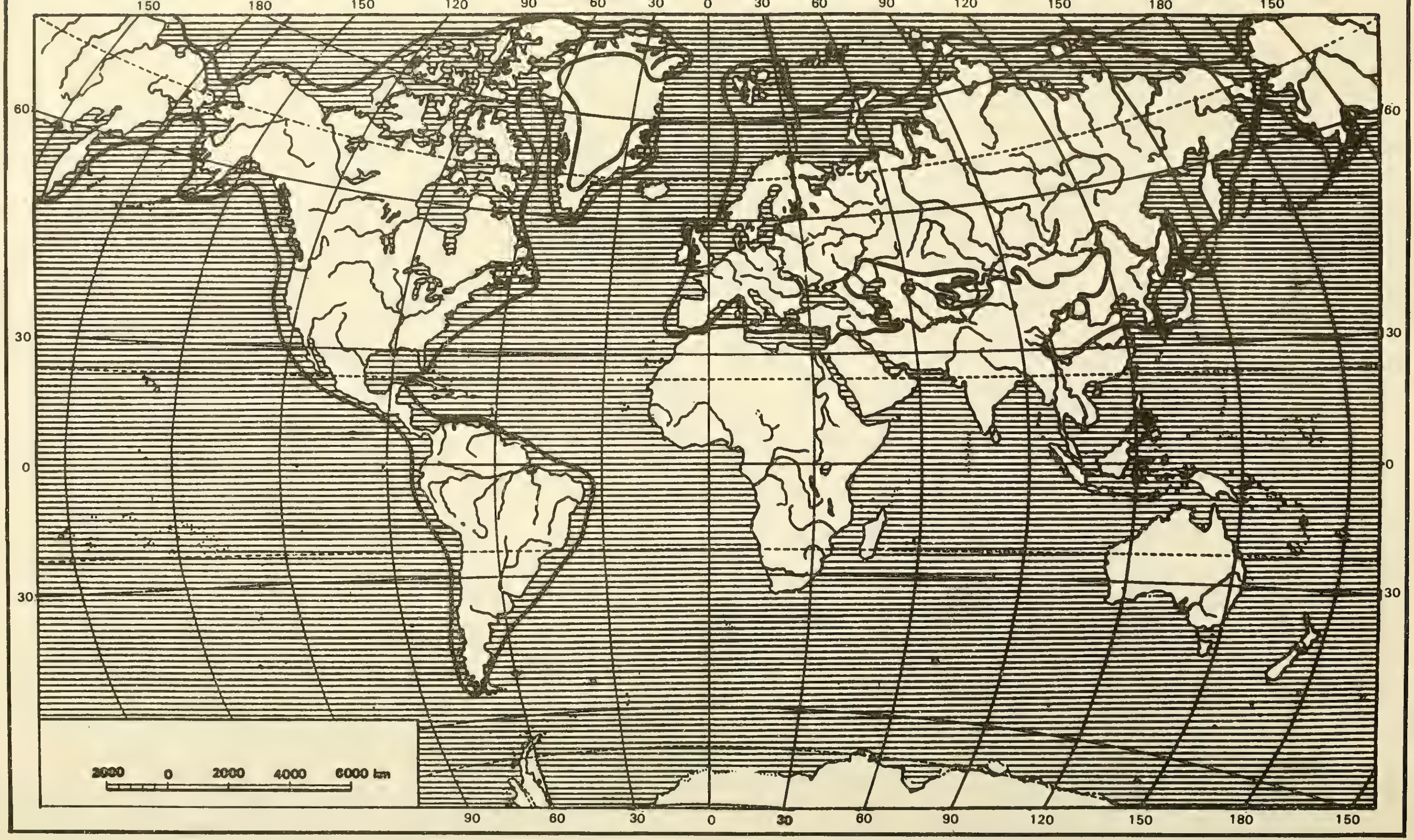

150
180
150
120
90
60
30
0
30
60
90
120
150
180
150
60
30
0
30
3000
0
2000
4000
6000 km

Fig. 57. Reconstructed geographic range of subfamily Odocoileinae (elk or telometacarpal deer). V.G. Heptner.

by a maximum number of genera and species. In the Old World only one genus (*Capreolus*) and one species of the subfamily are found. Two genera (*Alces* and *Rangifer*) are present in both the New and Old Worlds. In the New World Odocoileinae cover the entire range of the family; in Eurasia, they are distributed in the north up to the northern boundary of the family and in the south to the Mediterranean Sea, Asia Minor, northern Iraq, Ferghana, northern Mongolia, northeast China, Kansu, Szechwan, and Cheju-Do Island (for more details, see description of distribution of roe deer *Capreolus capreolus*).

The subfamily is well distinguished from all other subfamilies of Cervidae, but very close to subfamily Cervinae and even sometimes included in it.

Odocoileinae are known from the Lower Pliocene of Europe and Asia (Capreolini). In the New World they have been detected from the Pliocene.

Odocoileinae is understood here in its more or less traditional 174 format (according to Simpson, 1945, with the exclusion of genus *Hydropotes* from the subfamily), and not in the sense of Neocervinae Carette, 1922 (all Odocoileinae except *Alces* and *Capreolus*; Flerov, 1952).

The systematics of the group, mainly of South American forms, has attracted attention recently and their species composition and generic groupings, which until recently remained totally vague, have been delineated. Nevertheless differing opinions still persist. Simpson (1945) grouped the species (not including *Hydropotes*) into nine genera, Haltenorth and Trenze (1957) into seven, and Flerov (1952) into six. These differences are mainly due to downgrading some genera to the rank of a subgenus or simply discarding them. As far as the number of species is concerned, there are 15 according to the latest concepts (Haltenorth and Trenze, 1957), adopted in the present work (23 according to Flerov, 1952), which constitute about 42% of the species of the subfamily. In all, the subfamily comprises 12 genera (24% of all genera of the family) of which 7 are recent (41% of surviving genera of the family) and 5 extinct. Extant genera are: *Odocoileus* (subgenera *Odocoileus, Blastocerus,* and *Dorcelaphus:* four species); *Hippocamelus* (two species); *Mazama* (four species); *Pudu* (subgenera *Pudu* and *Pudella:* two species); *Capreolus* (one species); *Alces* (one species); and *Rangifer* (one species).

The first four genera form a single, fairly intimate group (tribe) of purely American forms, and three other separate, sharply isolated monotypic suprageneric groups (tribes). *Capreolus* is the lone form of the subfamily found in Eurasia, while *Alces* and *Rangifer* are encountered in the Old and New Worlds.

In the USSR three genera occur (about 43% of genera of the subfamily): reindeer—*Rangifer,* elk—*Alces,* and roe deer—*Capreolus,* with three species (20% of species of the subfamily). They constitute about 1.0% of the species of Russian fauna.

In the USSR Odocoileinae are distributed in tundra and forest zones, Crimean and Caucasian forests, and the mountains in the eastern part of Central Asia. The geographic range and population of one species decreased sharply in the last century, while the range of the others remained quite unchanged or only insignificantly altered.

Odocoileinae represent important game and table animals which are often protected. One species (reindeer) survives in both wild and domesticated states. (V.H.)

Genus of Roe Deer

Genus *Capreolus* Gray, 1821

1775. *Capreolus.* Frisch. *Natursyst. d. vierfüss. Thiere,* p. 3. This name, as well as all generic names given in this compilation (except *Dama*) are unsatisfactory from the viewpoint of nomenclature.

1821. *Capreolus.* Gray. *London Med. Report,* vol. 15, p. 307. *Cervus capreolus* Linnaeus, 1758.

1837. *Caprea.* Ogilby *P.Z.S.L.,* 1836, p. 135. *Cervus capreolus* Linnaeus, 1758. (V.H.)

Capreolus are telometacarpal deer of small size, very light and slender build, with a relatively short trunk, long neck, straight back, relatively small head, and long legs.

Hooves of middle toes small, narrow, and sharp; lateral hooves small, set high, and nonfunctional.

Skull relatively small, with a somewhat shortened facial portion. Nasals normal in length (roughly equal to length of upper tooth row; nasal and premaxilla not more than length of upper tooth row). Depression absent on anterior part of premaxilla. Nasal processes of premaxillae reach, or almost reach, nasals. Preorbital depression on lacrimal weakly developed, small, and with blurred outline. Ethmoid pit well developed. Processes for horns (or cornu) on frontals set back and up, and close together. Rear portion of vomer low and does not interrupt choanae.

Upper canines usually absent both in males and females, but seen exceptionally in males. Upper molars with relatively low crowns without supplemental columns on internal side. Dental formula:

$$i\,\frac{0}{3},\quad c\,\frac{0}{1},\quad pm\,\frac{3}{3},\quad m\,\frac{3}{3},=32.$$

Only males sport antlers, which are very small. Maximum length of antlers not more than 1.5 to 2.0 times length of head; however, often shorter than head. Antlers sometimes develop in very old females but are invariably small and usually irregular in form. Antler beam round in section and almost straight or only slightly curved backward at end; usually with three tines at terminal portion: one set forward, one upward, and one backward.[129] Exceptionally rear tine bifurcate (four tines on antlers) and, even more rarely, upper tine also (five tines on antlers). Antler beam with uneven surface, particularly rough on inner surface of the bottom half or third of antler length. Sharp tuberosities and often small elongated prominences form there. Antlers turn upward and backward and appear to be set almost vertically. Beam bases usually close-set and beams run almost parallel; sometimes slight or significant spread of antlers seen. Often they form a distinct layrate figure. Rosette relatively well developed.

Ears long and attenuate. Tail rudimentary and does not project out of fur and imperceptible in a living roe deer. Muzzle somewhat stunted and blunted and tip bare; bare field large and encompasses nostrils. Dewlap absent. Preorbital glands rudimentary and do not function. Hoof glands present only in hind limbs, in the form of a saccate invagination with a small opening. Tarsal glands well developed.

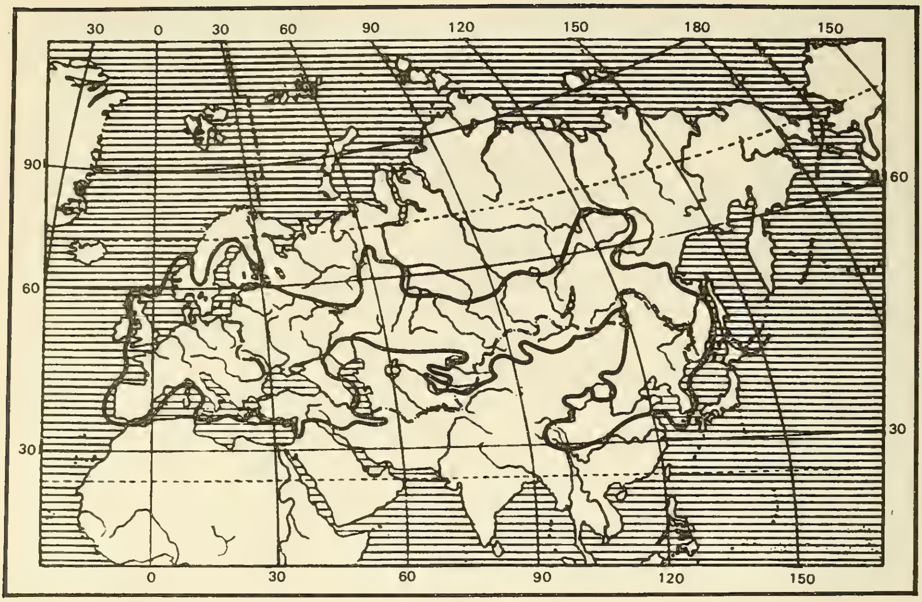
Coloration uniform; in summer coat bright and rusty and in winter dull and gray. Legs of same color as trunk. Large bright patch (speculum) occurs on rear side of thigh and around tail. Mane on neck absent. Coloration of young deer (in first coat) spotted. Female somewhat smaller than male. Teats four.

These animals inhabit deciduous and mixed forests in the plains and mountains, southern borders of tugais, forest-steppes, river valleys in the steppes, and sometimes even reeds. They are encountered in mountains up to heights of 3,000 m above sea level.

The distribution of the genus is restricted to Eurasia. Its geographic range (reconstructed) used to cover western, southern, and cen-

---

[129] Front tine usually considered medial, while upper one represents tip of the beam; rear tine set backward.



176 Fig. 58. Reconstructed geographic range of roe deer genus (*Capreolus* Gray) and species *Capreolus capreolus* L. V.G. Heptner.

tral Europe, including England,[130] Italy, and Sicily (absent in remaining Mediterranean Islands), and in the north up to the southern and central parts of the Scandinavian Peninsula, Asia Minor, Syrian region of the United Arab Republic and Palestine, northern Iraq, northern (Elbruz) Iran, the Caucasus, and Crimea.

In the east European plains and Asia the northern boundary ran along the Gulf of Finland, slightly south of Moscow, through the mouth of the Kama and the upper reaches of the Pechora, through Tobol'sk, Novosibirsk, the mouth of the Angara (upper Tunguska), and the northern extremity of Baikal. The eastern boundary rose up to 60° N lat. and, descending south, intersected the lower courses of the Amur and ran toward Tatarskiy Strait. The southern range covered the Korean Peninsula, northeast China, northern parts of
176 Mongolia (Pri-Hobsogol and Khentei) and the northern and northwestern parts of eastern and southeastern China (Jehol, Chakhar [?], Hopei, Shansi, Shensi, Kansu, and northern Szechwan). The western range encompassed the Altai range, Semireche, the Tien Shan

---

[130] Contrary to reports by some authors (Flerov, 1952), apparently roe deer never occurred in Ireland.

mountain system up to Ferghana valley, and Kazakhstan (northern half).

In general the typical zone of the temperate Eurasian belt represented the range of the genus. Compared with the reconstructed range described earlier, the actual present-day range at places has shrunk quite significantly or even broken down into individual pockets (see "Geographic Distribution" under roe deer).

The genus *Capreolus* stands very sharply isolated within the subfamily and exhibits no apparent close association with other present-day genera.[131]

This situation is largely explained by *Capreolus* being relatively ancient, one of the very oldest living genera of the family. Forms placed in this genus or proximate to it are already known in the Middle Pliocene (Europe).[132] Genus *Procapreolus,* which is very close to *Capreolus,* is known from the Lower Pliocene (according to some authors, even from the Upper Miocene) of Europe and Asia. There is reason to consider this group the parent stock of *Capreolus.*[133]

The distribution of fossil forms of the genus (reconstructed range) generally does not fall significantly beyond the limits of the present-day range. Species still different from extant species lived in the Gunz period and extant species appeared in the Riss-Wurm period (Flerov, 1950).

Three species (*capreolus, pygargus,* and *bedfordi*) were recognized in the genus until recently. In reality, however, only one species exists with some geographic variations (about 5% of species of
178 the family). The differences between some, especially between *capreolus* and *pygargus,* are so marked that they earlier prompted recognition of two "species" in the genus.

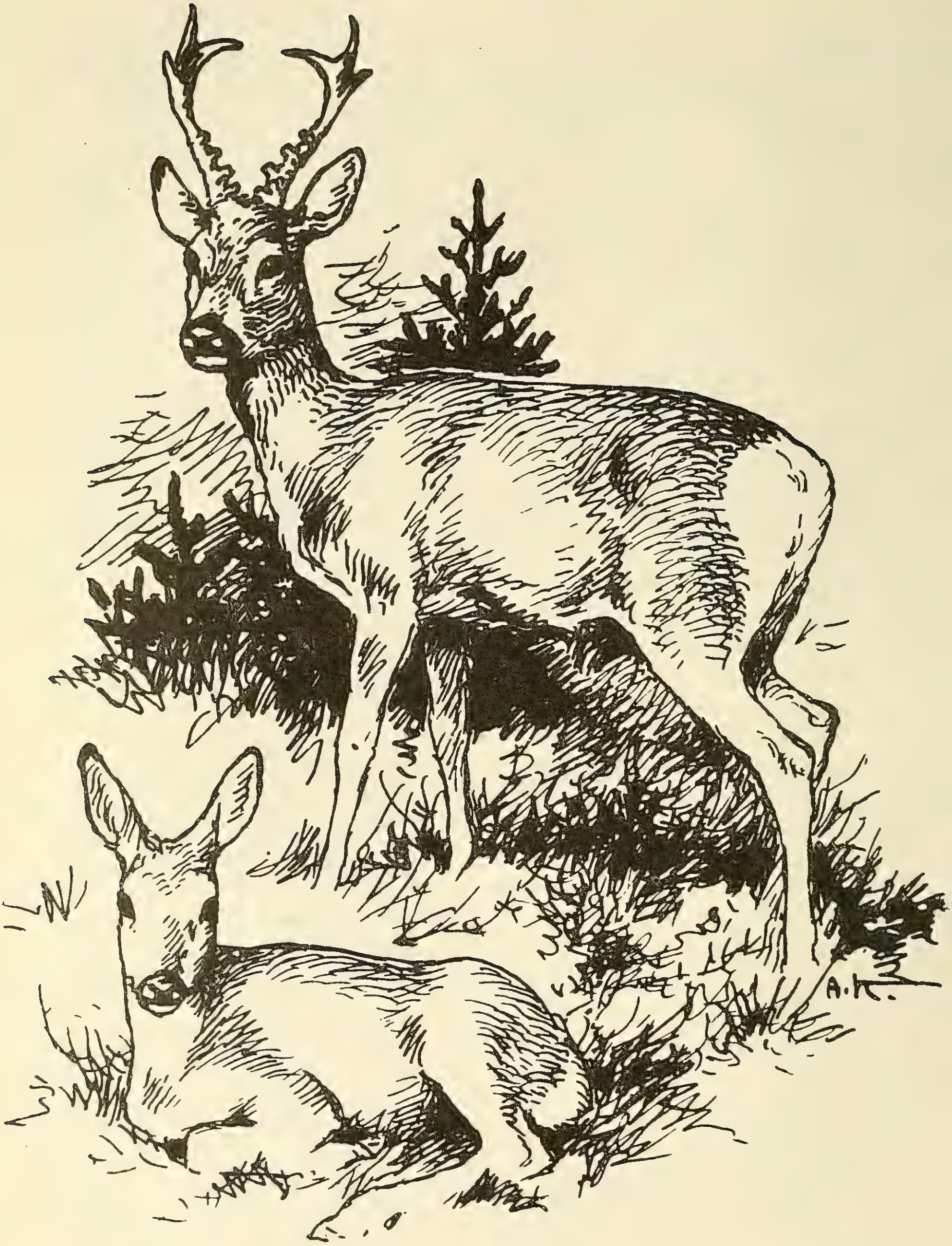
These are game and table animals caught mainly for their meat and hide. The antlers are used as decorative trophies and for making various articles. The animals are shot for sport and raised in controlled game farms.

---

[131] The view that *Capreolus* undoubtedly represent a connecting link between the groups *Muntjacus* and *Elaphodus* (Cervulinae according to some) and red deer (Cervinae) (Flerov, 1952) is hardly justifiable.

[132] Some researchers date fossil finds of true *Capreolus* to a much later period.

[133] Those who include *Capreolus* (along with *Alces*) in the genus of red deer (Cervinae) and separate this genus from American deer ("Neocervinae") place in a series the forms leading to *Capreolus* and *Pliocervus* (particularly Flerov, 1952) belonging to Cervinae. In any case the antiquity of the independent existence of this genus is beyond dispute.



177 Fig. 59. Siberian roe deer, *Capreolus capreolus pygargus* Pall. Sketch by A.N. Komarov.

One species, *Capreolus capreolus* Linnaeus, 1758, is found in the USSR and represents about 0.3% of all species of Russian fauna.

Roe deer represent table animals which at places are of great interest as objects of sport. Hunting them is prohibited in some parts of the range. (V.H.)

5. ROE DEER [134]

Capreolus capreolus Linnaeus, 1758

1758. *Cervus capreolus.* Linnaeus. *Syst. Nat.,* 10th ed., vol. 1, p. 68 Sweden.

1773. *Cervus pygargus.* Pallas. *Reise,* vol. 1, p. 453. Sok River, left tributary of Volga, former Samar province. Locality fixed as source of Sok, i.e., Bugulma-Belebey rise.[135]

1832. *Capreolus vulgaris.* Fitzinger. *Beitr. z. Landesk. Österreichs,* vol. 1, p. 317. Austria.

1843. *Capreolus caprea.* Gray. *List Mamm. Brit. Mus.,* p. 176. Proposed as substitute for *Capreolus* Linn.

1846. *Capreolus europaeus.* Sundevall. *K. Svenska Vetensk. Akad. Handl.,* 1844, p. 184. Proposed as a substitute for *capreolus* Linn.

1889. *Cervus pygargus mantschuricus.* Noack. *Humboldt.,* vol. 8, p. 9. Preoccupied by *C. mantschuricus* Swinhoe, 1864.

1906. *Capreolus tianschanicus.* Satunin. *Zool. Anz.,* vol. 30, p. 527. Kuldja, Tien Shan.

1907. *Capreolus transsylvanicus.* Matschie *Weidwerk in Wort und Bild.,* vol. 16, p. 224. Banat, Rumania.

---

[134] Roe deer have also been labeled "wild goat" or simply "goat". In Russia the male is called "kozel" and in Siberia "iguran"; the female is called "koza" and "kozlukha". "Kosulya" is evidently a variation of "kozulya". It has also been suggested that the name is derived from the slanted pupils of the eyes (Flerov, 1952); this interpretation of the origin of the term begs credulity.

[135] Sometimes the synonyms of this species include (Flerov, 1952) *Cervus ahu* as referenced by S.G. Gmelin (*Reise durch Russland,* vol. 3, p. 496, 1780). This name, applied to northern Iranian roe deer, could have had some nomenclatural significance as one of the earliest names except for a simple misunderstanding. The point here is that Gmelin's work does not mention the name *Cervus ahu* at all, either on the page referenced above or at any other place. On p. 496, in fact, the word "ahu" occurs in the margin but is cited as a local name and set in Gothic type. On pp. 496-499 Gmelin describes some animal which he had with him, distinctly a roe deer, and presents a drawing(Plate 56) but does not give it a scientific title. At the end of the text (p. 499) he states that Pallas, to whom a description of the animal was sent, wrote that it was an "ahu," evidently *Cervus pygargus.* Lydekker (1915), who used the name *Cervus ahu,* was evidently responsible for its introduction into nomenclature.

1908. *Capreolus bedfordi.* Thomas. *Abstr. P.Z.S.L.,* vol. 32, p. 645. Chaochen-Shan mountains 100 miles west-northwest of Taiyuan fu, Shansi province.

1909. *Capreolus pygargus* var. *ferganicus.* Rasevig, *Sem'ya Okhotnikov,* no. 8, p. 160. Precise location not indicated but evidently Ferghana. Mountains adjoining Ferghana valley from the north have been suggested.

1910. *Capreolus capreolus balticus.* Matschie. *Weidwerk in Wort und Bild.,* vol. 19, p. 263. "Vikherstgof, eastern Prussia."

1919. *Capreolus capreolus albicus.* Matschie. *Weidwerk in Wort und Bild.,* vol. 19. p. 263. Ezerki near Lissa, Poland.

1910. *Capreolus pygargus* Pall. var. *caucica.* Dinnik. *Animals of the Caucasus,* vol. 1, p. 73. Northern Caucasus.

179 1912. *Capreolus capreolus warthae.* Matschie. *Deutsche Jagerzeitung,* vol. 58, p. 801. Dombrovo to east of Bytom (Beiten), Poland.

1916. *Capreolus capreolus armenius.* Blackler. *Ann. Mag. Nat. Hist.,* vol. 18, p. 78. Sumela, near Trabzon, Asia Minor.

1916. *Capreolus zedlitzi,* Matschie, *Sitzungsber. Ges. Naturf. Freunde Berlin,* p. 172. Slonim to southwest of Grodno, Belorussia.

1935. *Capreolus capreolus ochracea.* Barclay. *Ann. Mag. Nat. Hist.,* vol. 15, p. 627. Korean Peninsula. (V.H.)

Diagnosis

The genus contains only one species.

Description

Size small, second only to musk deer from among Russian species of the family, and smallest of Russian deer.

Build extremely light and slender, trunk relatively short, and legs long. Neck quite long; that of males thicker than that of females. Head relatively short, highly wedge-shaped, and pointed in front. Back straight, hind legs somewhat longer than forelegs, and croup markedly higher than withers (design of jumping animals). Ears fairly large, long (longer than one-half of head length), and relatively broad. Bare patch at end of muzzle large, rising above the upper edge of nostrils, and surrounding them from the outside. Tail very short, does not project out of fur, and not visible externally. Preorbital gland poorly developed; hoof glands present; metatarsal glands well developed, with tufts of long, light-colored hair. Central hooves small and narrow and lateral hooves tiny and set high.

There are two main types of antlers, differing in structural characteristics but mainly in size.[136] Antlers of the European type are small, do not, or only slightly, exceed skull length (length up to 25, rarely 30 cm), and never exceed head length. An additional tine is very rare; usually only three tines present. Beams set very straight, sometimes almost parallel, or with a slight lyrate flexure. All tines usually set in the same plane. Bases of antlers close-set; rosettes large in diameter, adjoin or almost adjoin each other, and often closely pressed to each other. Distance between bases of beams usually not more than diameter of beam at that height. Osseous growths [pedicels] ("pipes") on frontals close-set, usually parallel, and sometimes tips quite close.

Tuberosities on beams developed mainly up to first tine; they are larger and coarser along inner and posterior surfaces of antlers. On posterior surface they grow up to the base of the last (third) tine. Tuberosities are well manifested but relatively small and usually do not exceed 1 cm in height even on large antlers.

Antlers of the Siberian type are large and, when fully developed, not less than length of skull, or longer, or even markedly longer. Antler length along main beam may reach 45 cm (or even more). Usually antlers of this type represent a simple but magnified replica of the European type with the difference that the osseous growths on the frontals are relatively more wide-set, their ends usually diverge, the rosettes are relatively small and do not touch each other, the antler bases are wide-set, and the distance between them is more than the beam diameter. Quite often even the distance between the rosettes is more than the antler diameter. Tuberosities are also more prominent.

In an extreme variation the Siberian type of antlers may be wide-set, the rosettes not large, and the distance between them not less than the antler diameter. The beams diverge sideways right from
180 the base. Often the beams are fairly straight and sometimes even form a lyrate figure. The antler tip often curves sharply inside; the rear tine also turns inside and quite often bifurcates. Even the forward tines reveal a tendency to bend in the same direction. The antler beam and tines are massive. The tuberosities on the beam are fewer than on the European type but more massive and prominent, their height often exceeding 2 cm. Some look like small irregular additional tines.

Sometimes not only the rear tines, but also the second ones (top of beam), are bifurcate and thus five tines occur. Sometimes the number of tines is even greater (up to 22), but this is purely a pathological phenomenon. Another type of pathological alteration also occurs, namely, an antler in the shape of a "wig", i.e., a solid osseous mass in the form of an "accumulation" covering the head and even the eyes. Small irregular antlers are occasionally seen in old or abnormal females. In general, among antlers of the Siberian type the same abnormal deviations as found among European forms are seen, but relatively rarely.[137]

---

[136] Innumerable abnormalities in development of antlers described extensively in game literature have not been included here. They are relatively rarely seen in the Soviet Union and occur mainly in central and western Europe where living conditions of roe deer differ significantly from those of the USSR.

The normal forms of the two antler types differ very sharply, providing a basis for the earlier division of roe deer into two species. At the same time the Siberian type of antlers differ in different parts of the range and there are also populations in which antler development is of an intermediate nature.

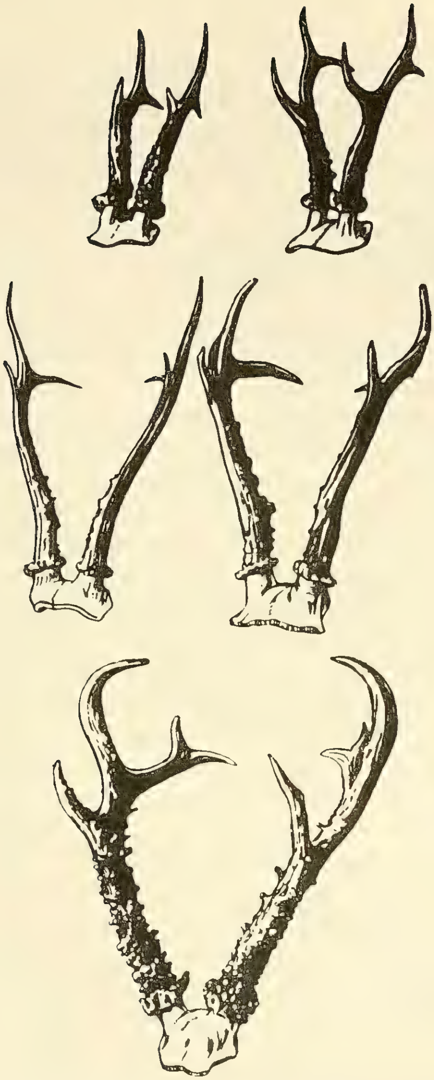
Full antler development is seen in roe deer older than three years. In fawns of the first year only tiny prominences ("pipes") are seen by autumn, simple unbranched "rods" in the second year, two tines after the second year, and three tines after the third. Later, normally, only an increase in size and weight of antlers occurs. Maximum antler development has been recorded at ages five to eight years. Deterioration sets in later and an overall reduction in size, simplification of design etc., associated with old age, is normal (roe deer live up to 15 years in captivity, but rarely beyond 10 years in nature).

The coloration of adult animals is fairly uniform. Only a large white or yellowish-white speculum stands out prominently in the caudal region, the width of which can reach 25 to 30 cm. At the top
181 the speculum does not spread above the caudal base. Its width is usually more than its height; sometimes it is nearly an inverted, heart-shaped form. The general shade of the winter coat of the trunk is gray, which shows some geographic as well as individual variability; it may be light gray or bluish-gray, or, contrarily, darker after acquiring a brown or cinnamon tinge. On the rear, along the upper border of the speculum, usually a dark band sharply demarcates the speculum from the back. The groins, abdomen, and inner sides of the limbs are whitish, often with a yellowish tinge. The outer surface of the limbs is generally of the same color as the trunk but turns slightly rusty downward.

The neck and head are generally of the same color as the trunk. There is often (especially in Siberian males) a light-colored patch of irregular shape on the throat. The ears are of the same color as the head on the outside, but often darker toward the tips; they are whitish or rusty on the inner side. A white spot of variable dimensions

---

[137] Additional data on antler variations in Siberian roe deer (diagrams) are available in Fetisov's work (1953).



180 Fig. 60. Antler types of roe deer inhabiting the USSR.
Top row—European roe deer from Carpathians (*C. c. capreolus* Linn.); others—Siberian roe deer from Pri-Baikal (*C. c. pygargus* Pall.). Original drawing, based on material from V.G. Heptner.

occurs on the chin and a dark spot on the lower lip toward the corner of the mouth. The upper lip is somewhat darker in color than the rest of the head. The winter hair coat consists of underfur and long (up to 55 to 65 cm) top and guard hair. The top hair is very curly, thick, and extremely brittle, due to which the coat is easily worn out and damaged. This is associated, as in some other deer, with the presence in the hair of large air-filled cavities (heat insulation). The hair is longer on the trunk, especially in the rear, shorter on the neck and head, and particularly short on the limbs. A mane and elongated hairs below the neck are invariably absent.

The summer coat is bright, rust-colored or rusty-red, being darker, fuller, and sometimes brownish on the spine. The trunk coloration lightens downward. The outer surface of the limbs is rust-colored, while the abdomen, groins, arm pit region, and the inner surface of the limbs are ocherous-white. The head and neck are generally of the same color as the trunk, the color of the head corresponding to that of the winter coat. Sometimes a white or light-colored spot occurs on the upper lip. The speculum is less prominent and has a yellowish tinge. The hair is much shorter than in the winter and is not longer than 35 mm in the rear of the trunk. On the head it is much shorter (on the forehead, it is somewhat longer, softer, and curly); the hair on the limbs is particularly short, only 12 or 13 mm long.

There are no sex-related differences in the winter or summer coat.

The main shade of color on the upper surface of young animals in the first few weeks after birth is rusty-yellow or rusty-cinnamon. The abdomen and the inner portions of the limbs are light ocherous. The color on the top of the head generally corresponds to that on the top of the body, the lower surface being somewhat lighter. Numerous white or slightly ocherous spots are scattered along the back and sides. They are usually so arranged as to form distinct patterns or bands. The two central bands are brighter, commence on the occiput behind the ears, and extend along the spine right up to the tail. Below them, along the sides, usually one or two more such bands commence from the shoulder blades and extend right up to the rear of the thighs. They are usually less distinct and the spots in them less sharp. On the thighs and partly on the shoulders spots are seen lower down. Young animals sport this coat for a short while and by age four months usually change over to an adult coat of uniform color.

Skull short and relatively broad; zygomatic width roughly about one-half length of skull. Facial part of skull short; line dividing skull into two fairly equal anterior and posterior portions runs roughly through midorbit. Premaxillae short, shorter than upper row of teeth, and taper gradually toward end; nasal processes come close to nasals or even up to them, but are not wedged between nasals and premaxillae. Anterior toothless portion of premaxillae short, usually shorter than length of tooth row. Nasals of moderate length, roughly as long as dental row, and wedged posteriorly into

182 frontals, almost at a right angle; anteriorly, each individual bone is deeply notched at the center, i.e., anterior end has a furcate appearance. Orbits relatively large. Lacrimals fairly large with rather large depression for preorbital gland, which occupies much of the frontal part of the bones even though very small. Tympanic bulla with an uneven surface and a short auditory meatus (its length invariably shorter than that of third upper molar). Anterior end of jugal not enlarged and does not reach lacrimal duct.

Upper canines absent in most animals; small canine seen rarely on one or both sides in some males.

In addition to marked age-related, sex-related, and seasonal variations, the size and weight of roe deer also undergo considerable geographic variability. Females are invariably smaller and lighter than males, usually weighing about 16% less than males in a given locality. The geographic differences are so great that members of the largest subspecies weigh roughly 1.5 or even 2.0 times more than members of the smallest subspecies.[138] Body length varies from 100 to 155 cm, height at withers from 75 to 100 cm, maximum skull length from 180 to 253 mm, and weight from 20 to 59 kg. (V.H.)

Taxonomy

The genus contains only one species. For more details see characteristics of subfamily and genus.

Geographic Distribution

Genus *Capreolus* is distributed in western Europe, western part of Near East, southern half of European part of the USSR, southern Siberia, the Far East, Kazakhstan, Tien Shan mountain range, Mongolia, northeast, east, and southeast China, and south to Szechwan.

Geographic Range in the Soviet Union

The range of roe deer in the Soviet Union is extremely extensive, covering all except the extreme west, southwest, and southeast parts. In the USSR the range is associated with the southern rim of the forest zone and forest-steppe, partly with the steppe zone, and montane forests. In its natural form the historic range was represented by one single zone although the dispersal of the animal at some places was sporadic or it deserted some places in winter or for a few years.

---

[138] Differences in linear dimensions are invariably much less and not so obvious. Difference in weight of antlers is, perhaps, relatively even more than that of body weight, since antlers are relatively larger in large Siberian roe deer and in some other forms of this type.

The boundaries of some parts of the range of roe deer, primarily its northern boundary, show a marked dependence on climatic conditions. The northern boundary in particular is associated with depth of snow. It has been demonstrated that a mean maximum snow height of 50 cm restricted the dispersal of species in northern European and Asiatic portions of the USSR (Formozov, 1946). This association is, however, only of a general nature; there is no strict correlation of range boundaries with the foregoing isogram. At several places the zone of regular habitation of roe deer extends considerably beyond, into places with a snow depth of 60 or even 70 cm (western Pri-Urals and western Siberia). Sometimes a temporary shift in range beyond this line took place for several consecutive years due to various causes, for example, a series of less snowy winters and reduced interference by man (Nasimovich, 1956). Irregular visits of some individuals or groups of animals beyond the above-mentioned isogram into places where conditions of living are favorable is a fairly regular phenomenon. Nevertheless, the importance of snow for demarcating the northern range boundary is fairly clear; significant northward projections of boundary are associated with relatively less snowy zones (Pri-Baltics, Urals, Trans-Urals, Pri-Baikal, and others), and withdrawal southward in more snowy zones (central zones).

During the historic period the range of roe deer underwent significant variations. 183 Essentially these changes are similar to those seen in the case of wild boar described earlier. This is largely explained by the similarity of the northern range boundaries for both species and the causes of their fluctuations under the influence of the same set of factors (hunting by man and at times by predators) influencing identical peculiarities of the species in identical ecological conditions (response to snow). In many respects these differences are quite diverse both in nature and magnitude.

The main range changes in roe deer in the period under discussion are as follows. The natural range prevailing evidently up to the seventeenth and early eighteenth centuries was continuous and extended from the western boundaries of the [Soviet] state through the basins of the Dnieper, Don, and Volga into the Urals, and farther into western Siberia up to the Pacific Ocean. In the south the range ran into the Crimea and the Caucasus. Later, in the nineteenth century, the range began to shrink, mostly in the European part of the Soviet Union and also in the Urals and western Siberia. This process was considerably intensified in the latter half of the nineteenth century. It proceeded particularly intensely in the twentieth century. The culmination of this process and a corresponding reduction of range occurred in the 1920's. An essentially similar state prevailed by 1930, although a tendency toward expansion was observed at some places.

By then, roe deer were absent in much of the European part of the USSR. They evidently disappeared from considerable areas to the east in western Siberia, in Kazakhstan, etc. Thus, at that time the range not only contracted but was also broken down into several zones which were totally or partly isolated from each other. The resultant zones could be called the *western, Crimean, Caucasian, Ural* (partly also west Siberian), *Siberian-Far East,* and *Middle Asian* locales. Division of the range into western, Crimean and Caucasian zones and separation of the Ural-Siberian zone occurred long ago, while isolation of the Ural and Siberian-Far East zones, and evidently that of the Middle Asian zone as well, occurred in the first two decades of the present century.

Commencing from the 1930's an expansion of the range of roe deer has been observed, colonization of the animal at some places being quite rapid. The most marked changes occurred evidently in Yakutia, Pri-Urals, and western Siberia. The Ural region of habitation fused with the Siberian-Far East and the Middle Asian habitat also joined later. However, fusion of the western, Caucasian, Crimean, and Ural ranges has not occurred.

Reconstructed range. The northern boundary of the reconstructed geographic range[139] in the USSR ran northwest along the shore of the Gulf of Finland, encompassed the Karelian Isthmus, and extended into Finland.[140] Later it ran along the southern bank of Lake Ladoga roughly up to the mouth of the Syasa. From there it turned southeast and later east, running through Tikhvin, the Rybinsk reservoir, and Yaroslav (or slightly more northward, toward Danilov), to Kostroma, and the region slightly north of Gor'kii (Balakhn), or close to Semenov. From there, for some inexplicable reason, it turned toward Kazan or slightly more north.

Some of the more advanced peripheral points through which the boundary line extended represented the limits of transgressions of

---

[139] In the present case the term "reconstructed geographic range," as will be explained later, connotes a meaning different from the normal sense; the reference is more to the maximum range over the historic period.

[140] In the Karelia Isthmus roe deer were sighted rarely and occurred there only as a visitor. The boundary of the more regular habitat ran along Neve.

the animal or the maximum northward advancement of the boundary in several years with poor snowfall. This pertains primarily to deer occurrence in Yaroslav and Kostroma districts and in the region between Kostroma and Gorkii. Nevertheless, there is no doubt that the boundary of regular habitation of the animal in the Yaroslav-
184 Gorkii section also came quite close to the above line; roe deer colonized fairly extensively in the Moscow district even in the sixteenth century, and still survived in Podol and Serpukhov districts and even the Bogodor district in the latter half of the last century, and were seen around Moscow itself. Sightings are also known from around Pereslav-Zalessk; roe deer existed normally and in considerable numbers even quite recently in the Gorbatov region, southwest of the Oka mouth, on its right bank. They resided permanently north of Tula (Tula Zaseka) and in regions adjoining the Volga from the south, in the zone between the Oka mouth and Kazan (southern part of Nizhegorod and Simbir provinces).

From Kazan the boundary ran east roughly along 56° N lat. or along the Kama, emerged toward the mouth of the Beloe into the Kama, and departed beyond the Kama. From there it turned steeply straight north and ran along the Pri-Urals through Perm,[141] Dobryanka (about 80 km north of Perm), Kizel, and Cherdyn' into the sources of the Pechora, up to the discharge of the Ilich into the Pechora (62°30'). Nevertheless, the region of the source of Pechora evidently is only a region of occasional visits by the animal.

In the Urals per se the northern boundary of the range fell on the latitude 62° N lat., evidently even slightly more north at 62°30' N lat. Sightings have been reported in the eastern foothills up to 64° N lat. (upper course of the Lyapin, a tributary of the Severnaya Sosva). It is possible that animal visitations may have extended even farther, but there is no precise information about this. These places represent some of the northernmost points of occurrence of roe deer.[142]

In the Trans-Urals the range boundary turned sharply south from the upper reaches of the Lyapin in the upper reaches of the Severnaya Sosva, and from there to the east or southeast to the Ob', where it merged roughly at 61°40′ or 62° N lat. (Leushi), i.e., markedly north of the mouth of the Irtysh. From there the range ran south along the left bank of the Irtysh up to a point slightly south of the confluence of the Tobol with the Irtysh. Later it turned sharply east, intersecting the Ishim slightly above its mouth and the Irtysh below Tara. After passing through the northern parts of the Barabinsk steppe, it intersected the Ob' and Tom' slightly south of the latter. Roughly at the same latitude the boundary ran toward Krasnodar, but slightly short of reaching it rose up to 58° N lat. on the left bank of the Yenisey (regions of Bol'shaya Murta, Kazachinsk, and Pirov). Crossing over at this level onto the right bank of the Yenisey, the boundary turned east along the Angara, intersected it somewhere below the Ilim mouth and ran farther through the Katanga River (at the source of the Podkamennaya Tunguska to the northeast of the Ilim mouth), roughly around 59°30′, and through the source of the Nepa (tributary of the Nizhnaya Tunguska at its source).

---

[141] The position of the range boundary between Menzelinsk, the Ufa River, and Perm is not clear. Possibly, it proceeded roughly along the Kama.

[142] The range boundary in the European part of the USSR and the Urals is based on data from M. Bogdanov, 1871; Lavrov, 1929; Bobrinskii, 1944; Middendorff, 1869; Chernaya, 1860; Kessler, 1850; Formozov, 1946 and 1947; Severtsov, 1955; Ognev and Vorob'ev, 1924; Danilov, 1947; Nasimovich, 1956; Fedesov and Nikitin, 1951; Kuklin, 1951; Kirikov, 1952, 1953, and 1955; Heptner. Morozova-Turova and Tsalkin, 1950; Korneev, 1952; Serzhanin, 1955; Elpat'evskii, Larina and Golikov, 1950; Schwarts, Pavlinin and Danilov, 1951; Popov et al., 1954; Flerov, 1952; Eversmann, 1850; Pallas, 1811; Demidov, 1940; Turkin and Satunin, 1900; V.N. Skalon, 1946; Siivonen, 1953; Kalela, 1948; and others.

From there, in a manner not known for certain, but evidently following the Lena, the boundary turned northeast and crossed onto the left bank of the Lena, above (west of) Mukhtuya roughly at 113 to 114° E lat.[143] Later it ran into the Vilyui in the region of western Suntar. Thus, in this part of Yakutia, roe deer lived in the basin of
185 the lower reaches of the left hand tributary of the Lena and Nyuya, most probably in much of the basin, if not the whole of it. On intersecting the Vilyui the boundary encompassed the left bank of the river within the Suntar bend and ran roughly toward the mouth of the Markha. Farther away in the east it turned generally along the Vilyui possibly also encompassing the lower reaches of its left hand tributaries, and emerged into the Lena in the region of the mouth of the Vilyui, i.e., around 64°, or slightly more north.[144] It is possible

---

[143] Abundant information is available for some parts of the range of roe deer in the zone between the Yenisey and Baikal and for western, northern, and northeastern Pri-Baikal; it exceeds the information available for several regions in the western parts of the Soviet Union. However, much of the information is contradictory. Because of complex orography, different local conditions of snowiness, and so on, the range there can be regarded as extremely complex and, what is more, gaps are evident in this information. Moreover, changes there could vary quite intensely in different years. Information is absent or scanty for vast expanses, for example the regions of the Kirenga, Chai, Chui, and Mama basins, and elsewhere.

[144] In Yakutia roe deer occupied the "Vilyui" region, Lensk, Olekminsk, Ordzhonikidzev, Gornyi, and Yakutsk regions (Belik, 1953; and other sources). According to other authors (D.U. Ivanov) roe deer did not go beyond the Vilyui in the north and did not reach even up to its mouth (known as Kobyai or Kobyaitsa).

that there the boundary ran even more northward since encounters with roe deer are known in the area of Syalakh (Sylakh) in the Zhigansh region at 66° N lat. This is the northernmost recorded habitat of roe deer in the USSR.

On the right bank of the Lena roe deer occupied nearly the whole area between the Lena and Amga, in the north up to the latitude of the Amga mouth into Aldan, and in the east and south up to, or almost up to the Amga, from the mouth up to the source. From the source of the Amga the southern boundary on the right bank of the Lena turned southwest and crossed straight to the Olekma. Thus, in Yakutia the range of roe deer was like a large promentory to the north. Such a distant penetration of roe deer into northern Yakutia, apart from the reasons stated above (snow), was associated and largely coincided with the entire complex of forest-steppe and steppe topographies developed in this part of Yakutia (along the Vilyui).[145]

Upon crossing the Olekma the boundary along this river turned south toward the western extremity of the Stanovoy range. From there it turned sharply east and, for some inexplicable reason, extended toward the Amur basin[146] evidently along the northern slopes and foothills of the Stanovoy range through the uppermost reaches of the Aldan (Timptonsk region of Yakutia with the center at Chul'man), the watershed of the Gonam and Algama, and the upper reaches of the Uchur. The range, however, did not cover the Aldan-Uchur range (K.A. Vorob'ev).

In the east the boundary did not reach the Pacific Ocean at these latitudes, but on intersecting the Stanovoy range or the western extremity of the Dzhugdzhur turned southeast and south, encompassing the upper reaches of the Uda and running along its right hand tributary, the Galam (roughly at 54°30′ N lat. and 133°30′ E long.; V.H.). From there the boundary line excluded the lowermost reaches and mouth of the Amur outside the range, and ran into the mouth of the Amgun on the Amur, and from there evidently through the region of Lake Kiza toward Tatarskiy Strait, south of De

---

[145] There is not much accurate information for northern Yakutia where roe deer became established in the last decade. Nevertheless, the data and map given here represent significantly more accurately the actual picture of the range north and east of Lena than those published earlier (Lavrov, 1929; Bobrinskii, 1944; Flerov, 1953).

[146] Information given for the Aldan basin is based on reports which are partly inaccurate and in which geographic names have obviously been distorted. Thus, it has been shown (V.N. Skalon, 1937) that roe deer were caught on Meguskaya River and also on the watershed of the Gonata and Algata. Middendorff (1869) reports that roe deer were found only on the southern slope of the Stanovoy range.

Kastri Bay, roughly at 51°. Sakhalin did not fall within the range.[147]

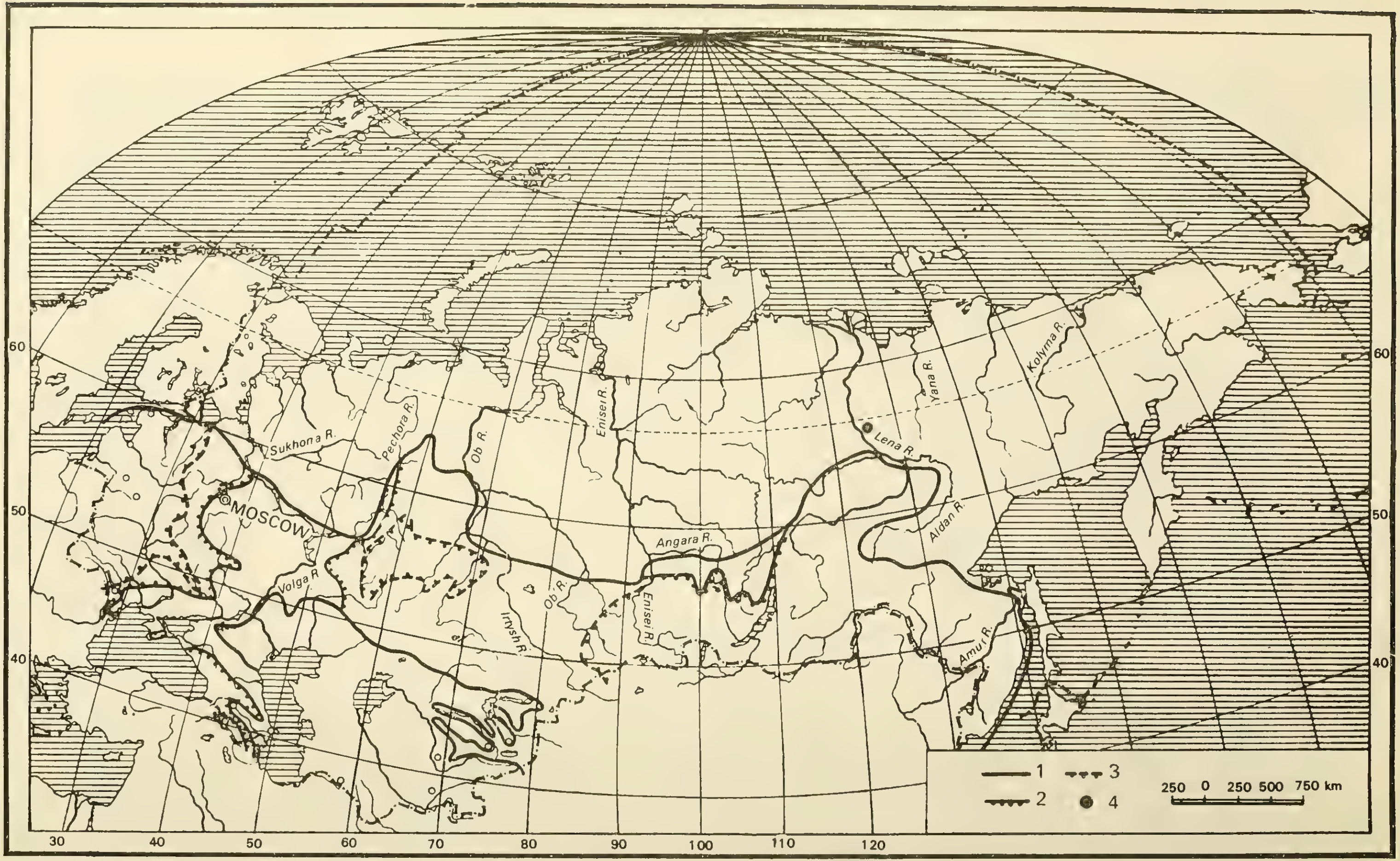
The southern boundary of the reconstructed range of roe deer in the European part of the USSR evidently traversed the Black and Azov Sea coasts. Although direct references to this are not many, based on the sum total of information about the nature of the Soviet south in the past and the ecology of roe deer, there is every reason to believe that roe deer occupied not only the forest-steppe, but also the whole of the steppe zone. The distribution in the latter was, of course, sporadic even as it is now in Kazakhstan (see below). There is
187 no doubt that roe deer performed even longer migrations through the steppe (covering several dozens and hundreds of kilometers). This part of the range crossed directly into the Crimea and joined with the Caucasian part; in the south, in the Trans-Caucasian region, the range ran beyond the state boundary and also obviously covered the steppe region of eastern Trans-Caucasus.

In the zone falling between the Don, Altai, and Tien Shan, i.e., in the region adjoining the northern part of the Caspian Sea, in Kazakhstan and Middle Asia, the southern boundary of the natural range was fairly complex and its features are still not wholly understood. In general the range there encompassed not only the steppe but also the rim of the semidesert, or even the desert zone. It is quite natural that the dispersal of the species there also remained sporadic. The mountain systems mentioned before also fell within the range.

Adequate positive information is not available about the dispersal of roe deer in the past in the Pri-Caspian region and any boundary drawn would only be approximate. Commencing in the west on the coast of the Caspian Sea in the region of the estuaries of Kuma and lower Manych, the range boundary evidently passed along the Don or its left hand tributaries, bypassed from the west the semideserts on the right bank of the lower reaches of the Volga, and ran toward the Volga in the Stalingrad region. It is possible that roe deer descended right up to the sea along the Volga valley in the distant past. In some manner not yet clearly understood the boundary turned east from the Volga and evidently covered the Eruslan basin and the region of the upper and middle Uzen'. It is highly

---

[147] The northern boundary of the range of roe deer in the Asiatic part of the Soviet Union has been taken from Nasimovich, 1955; Yanushevich and Blagoveshchenskii, 1952; Slovtsov, 1892; Zverev, 1937; Kopylov, 1948 and 1950; Favorskii, 1936; Podarevskii, 1936; Abramov, 1954; Formozov, 1946; Tugarinov, Smirnov and Ivanov, 1934; Troitskii, 1930; Novikov, 1937; Yakovlev, 1930; Gassovskii, 1927; Middendorff, 1869; Skalon, 1937 and 1946; Turkin and Satunin, 1900; Schrenk, 1859; Flerov, 1935 and 1952; Maak, 1859; Abramov, 1954; Belyk, 1953; Fetisov, 1953; Lavrov, 1929; and some others (including the unpublished material of D.U. Ivanov and A.A. Sludskii).


MOSCOW
Sukhona R.
Pechora R.
Volga R
Ob R.
Irtysh R.
Enisei R.
Angara R.
Lena R.
Yana R.
Kolyma R.
Aldan R.
Amur R.
60
50
40
30
40
50
60
70
80
90
100
110
120
1
2
3
4
250 0 250 500 750 km

probable however that along these rivers it descended even more southward to the Kamysh-Samar lakes. From there the boundary ran along the Ural [River] to Uralsk. Evidently, as along the Volga, roe deer descended far south along the Ural valley also.

Farther away in the east the range covered a considerable part of Kazakhstan where roe deer were distributed (partly surviving even now) extremely sporadically, but extensively.[148] Commencing at Uralsk the southern boundary of the range ran southeast, covering from the south the Ilek, including the Khobda basin, a tributary of the Ilek (Khobdinsk, Aktyubinsk region), and later left at Dzhurun (about 100 km south of Aktyubinsk). From there it turned almost straight east, passing roughly between the towns Irgiz and Turgay and later, slightly descending southward, encompassed the Ulutau mountains from the south.[149]

Traversing through the upper part of the Sarys River and later through the regions of the Aktau and Ortau hills along the northern coast of Lake Balkhash at a distance of about 100 km from it, roughly at the meridian of the eastern extremity of the lake, the boundary turned south and ran toward the lake. The range left out
188 not only the Chingiztau and Tarbagatai but also the whole of the

---

[148] In the steppes roe deer occupy not only large forest masses but also small groups of isolated forests, ravines, areas with shrub thickets in the plains as well as in hilly terrains, forests in river valleys, sometimes overgrown river banks, and reed thickets of lakes. They often live in very small sections even when separated from each other by several dozens and even hundreds of kilometers of open steppe (pine forests of Ara-Karagay, Aman-Karagay, Naurzum-Karagay, forest sections around Aktyubinsk, Ulutau mountains, Kokchetav, Kent mountains, Kuu. Karkaralinsk, Airtau, and others).

[149] The information that in the Turgay basin region roe deer were confined to and hunted in the southeastern part, i.e., east and northeast of the Aral Sea is clearly incorrect (Turkin and Satunin, 1900). Turkin in *Zver'e Rossii* (Animals of Russia) used information about fauna and hunting submitted by the provincial governments to the Commission for preparing hunting legislation, of which Turkin was a member in the 1890's. The provincial governments, however, did not always examine well the data given them. In the present case some confusion with saiga seems indicated.

---

186 Fig. 61 Geographic range of roe deer, *Capreolus capreolus* L. in the USSR and some of its modifications (scale in km).

1—boundary of reconstructed range and its maximum expansion in the last decade (mid-1950's); 2—boundary in mid-1950's where it does not coincide with reconstructed range; 3—boundary during its maximum reduction in 1920's (roughly by 1930) in the European part of the USSR, Urals, and Siberia; 4—places of roe deer visits toward Syalakh at 66°N lat. (south of Zhigansk on the Lena). Additional details given in Figs. 62 and 63. V.G. Heptner.

Alakul'sk basin, and crossed the Dzhungarsk Alatau into the Central Asiatic part of the range.

Thus in Kazakhstan roe deer occupied not only the entire steppe zone in general, but also very significant portions of the semidesert zones, penetrating even into the deserts. As mentioned before, in these zones they took shelter in some of the apparently least suitable areas. Elevated sections with trees or at least shrubs were the most favorable. It is interesting that in Kazakhstan roe deer penetrated far into the regions of dispersal of such typical steppe, semidesert, and desert ungulates as saiga, goitered gazelle, kulan [wild ass], and wild horse.[150]

The range of roe deer covered a considerable region in the mountains of Middle Asia in the east. The boundaries of this zone are, however, as yet poorly understood and can only be generalized. A fairly accurate picture can be drawn only in the north. There, in spite of its fairly complex features, it encompassed the Dzhungarsk Alatau, intersected the Iliisk basin, ran into the Trans-Iliisk Alatau, and later into the Kirgizian mountain system. Along the Karatal and Ili Rivers the range formed narrow projections right up to Balkhash and along the Chu up to the floodplains of its estuary zone. The Chu-Iliisk mountains in the north, including the Dzhambul mountain group, fell within the range. Farther away the boundary made a prominent projection northwest, encompassing the Karatau mountains. From there, in a manner not precisely understood but obviously complex, it proceeded south, bounded on the west by the mountain ranges of the Tien Shan system, later ran along the northern slopes of the Ferghana valley, turned east, and evidently ran toward the state boundary with China, exiting from Soviet frontiers. The southern boundary of the range of roe deer in the mountains of Middle Asia evidently proceeded in the same manner.[151] Information is available that the habitat of this species extended more southerly, in the Gissar mountains (Flerov, 1935; Turkin and Satunin, 1900) and even the Darvaz range (Lavrov, 1929). These statements, sometimes with additional data, are based on information provided by G.E. Grum-Grzhimailo (1886, pp. 92 and 93). The first to use this information was Turkin, who misinterpreted it (Turkin and Satunin, 1900). Like Turkin, other researchers also erred because though they referred to the original source they evidently used Turkin's text. Yet from the original data of Grum-Grzhimailo it is absolutely clear that what he had in mind were wild goats (*Capra*—evidently *C. sibirica* and *C. falconeri*).[152] The assertion that "roe deer inhabit the Zeravshan mountains" (Flerov, 1935) has not only not been confirmed but is contradicted by new data on the total absence of roe deer within Tadzhikistan (V.I. Chernyshev).[153]

---

[150] The range boundary of roe deer in the section under description is based on data from V.G. Heptner; Kuznetsov, 1948; E.I. Strautman, 1953; Sedel'nikov, 1903; Antipin, 1941; Lavrov, 1929; Turkin and Satunin, 1900; Derevyagin, 1930; Lentovskii, 1928; Korsakov, 1938; Selevin, 1925; N.V. Pavlov, 1931; and others (mainly the unpublished data of A.A. Sludskii).

[151] References to the northern part of the eastern Bukhara basin, Trans-Caspian region, and Tien Shan south of the Pamir (Flerov, 1935) have been omitted in the present study.

189 Along the Syr-Darya, at least in the period under consideration, roe deer were evidently absent and the suggestion of their occurrence in the valley above Kzyl-Orda (Antipin, 1941; map) is unfounded. In the very distant past it may perhaps have been sighted on the river but there are no references to this possibility. Information about the occurrence of roe deer in the Amu-Darya estuary (Lavrov, 1929; according to report of Manteifel') is incorrect. Statements that in Samarkand district roe deer thrive in abundance and "In the Trans-Caspian district sizable numbers lived in the Krasnovodsk region" (Turkin and Satunin, 1902) are erroneous and evidently the result of confusing mountain goat and goitered gazelle (see footnote 152). Also erroneous, in part simply fantastic is the suggestion that roe deer inhabited the Bol'shoi Balkhan early in the last century and were sighted even in 1941 and 1942 (Bazhanov, 1945).

Throughout the stretch from Semirech'ya to the Pacific Ocean the range of roe deer extended up to the state boundary in the south.[154]

---

[152] Lavrov (1929) states that Grum-Grzhimailo in 1886 pointed out the presence of the deer in Gissar (! V.H.) and Darvaz mountains, and that residents in those days were well acquainted with it. Grum-Grzhimailo's text states: "In the Gissar mountains occur two species of goats, but no kind of deer. There are also none in the Darvaz and nearby, where the residents are acquainted only with the kiik, consequently, once more in them there are only mountain goats" (p. 92) "*Capra* sp.?—kiik in Kirgiz" (p. 93).

[153] Yet it is quite possible that roe deer inhabited or could have occurred in the Alaiskii mountain range. In the zoological museum of the Academy of Sciences there is a skull of a specimen caught by Grum-Grzhimailo on the northern slope of the Alaiskii range on Dzhusala River in 1889. It has not been possible to establish precisely the place at which the animal was caught. It is highly probable that the place of capture was the eastern or northeastern extremity of the mountain range where it adjoins Ferghana, i.e., in the region of the sources of the Kara-Darya or in the southern part of the mountains which surround the Ferghana valley from the east. This does not alter the conclusion drawn above about the southern range boundary of roe deer in the mountains of Middle Asia. In the same part of the mountains which enclose Ferghana valley from the south roe deer were evidently absent, at least in the region south of the city of Ferghana (V.G. Heptner).

Geographic range in the period of utmost depletion. As shown above, in this century, and in particular in the nineteenth, due directly to the extermination of animals over considerable regions the range underwent steady shrinkage. Separation of the Caucasian and Crimean parts of the range from the European occurred long ago. It took place notably in the latter half of the last century and the early part of the present century. The maximum reduction of the area of the range occurred in the 1920's. By this time the range was already divided into several smaller parts, as mentioned before, and their outlines in most cases cannot be determined precisely.

The eastern boundary of the western habitat of roe deer commenced at the eastern extremity of the Gulf of Finland and formed an irregular and fairly complex line before turning south and leaving the USSR to enter Rumania. From Leningrad the boundary proceeded east along the Neva and the southern bank of Lake Ladoga roughly up to the mouth of the Syasa. Visits into the Karelian Isthmus did take place but very rarely. From the Syasa estuary this line, without crossing the river in the east, turned south and ran toward Borovichi, later slightly southeast toward Vyshnemy Volochek, and from there straight south into Ostashkov. Later it dipped slightly southwest into Velikii Luki from where it turned south-southeast toward Smolensk and Zhizdr, and later followed a fairly steep westward arc, running initially southwest into the Novozybkov region, and later still turned steeply eastward toward L'gov, and south-southeast of it into Graivoron, more to the west of Belgorod.

From there the long penetration of the range east and southeast into the Kharkov region commenced. From Graivoronsk the boundary line proceeded southeast of Valuika, bypassing Kharkov from the north, turned to Chuguev, and later passed into the Izyum region. From there it turned sharply northwest and proceeded to Zmiev and Krasnokutsk (west of Kharkov, south of Akhtyrka), and later into the region south of Konotop. From there the boundary turned west, passed south of Nezhin and, taking a steep southwestern or even southern direction, proceeded toward the Dnieper south of Kiev. It traversed some distance along the river and intersected it evidently at about 50° N lat.

On the right bank the boundary ran almost straight south into

---

[154] The range in the Tien Shan and Pamir-Alaiskii systems is based on data from E.I. Strautman, 1953; Kuznetsov, 1948 and 1948a; Antipin, 1941; Turkin and Satunin, 1900; Grum-Grzhimailo, 1886; Flerov, 1935 and 1952; Lavrov, 1929; and other sources, including original data from V.G. Heptner and V.I. Chernyshev.

the region south of Korsun'-Shevchenkovsk. It then ran farther southwest, south of Uman, intersected the Bug somewhere in the region of Pervomaisk and ran into Moldavia, evidently passing there in the region of Kishinev and later into Rumania. Outside the foregoing boundary lay a very large pocket of habitation of roe deer north of Voronezh in Usmansk forest (Voronezh preserve). Further-
190 more, there were evidently some small pockets of habitation of roe deer on the right [west] fringe of the Ukraine, for example in the Black Forest of Kirovograd district, and on the left at Novomoskovsk near Dnepropetrovsk. The occurrence of deer at Izyum was also in the form of an isolated pocket.

The above boundary line has been described only schematically.[155] Information on the range of roe deer is not only scanty, but also for the period in question the contraction of the boundary was very indeterminate. All along the eastern edge of the range, over a goodly portion if not all of it, roe deer populations were sporadic and small pockets of these animals often widely separated. The number of animals in these pockets, since the total population of the species was far from large, was understandably quite small. The boundary of this zone varied notably in different years due to animal extermination at some places and range expansion in others. At places colonization commenced evidently even during the 1920's but was observed somewhat later. Finally, there are records of visitations east of the above line, often over fairly considerable distances. In the west the boundary of this region extended up to the Baltic Sea and into the Carpathians and Rumania.

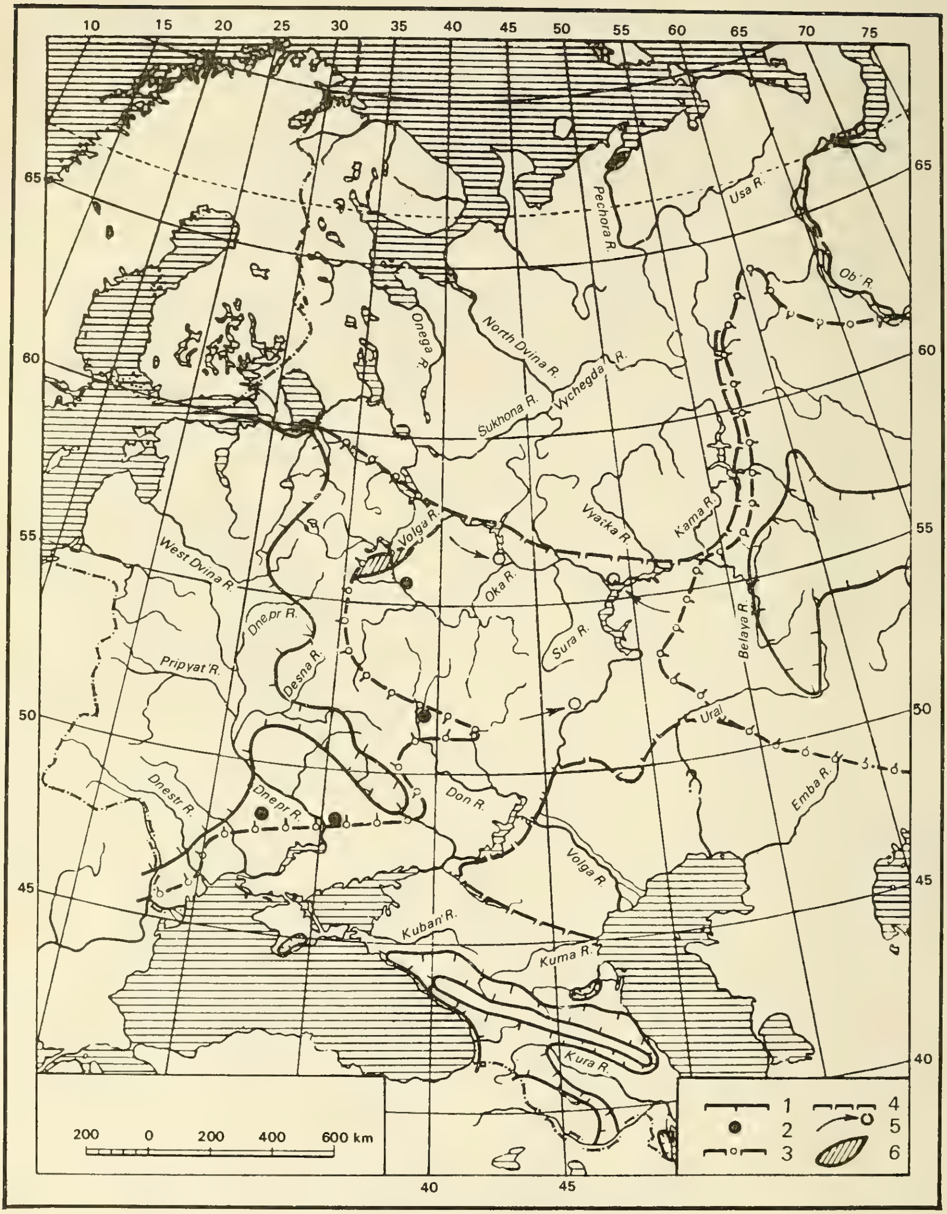
Distribution in the Crimean region was restricted to a small area in the forest section of montane Crimea.

Distribution in the Caucasian region during the period under consideration was roughly the same as in the 1950's (see below).

Distribution in the Ural-western Siberia was fairly complex. The westernmost point lay in the region slightly east of Ufa. From there the boundary proceeded north and northeast, generally along the Ufa River or parallel to it, but barely west of it. From Krasnoufimsk it turned northeast and ran into the upper reaches of the Chusovoi and ascended along the Urals roughly up to 58° or slightly more northward. It then arced southward, turning southeast and later east, through Irbit, north of Tyumen, and south of Tobol. Running in that direction and slightly dipping south, it reached the vicinity 72° E long. From there, forming a promentory jutting into the east,

---

[155] Mainly according to data of Lavrov (1929), which provide additional details not given here.


10
15
20
25
30
35
40
45
50
55
60
65
70
75
65
60
55
50
45
40
Usa R.
Pechora R.
Ob' R.
Onega R.
North Dvina R.
Vychegda R.
Sukhona R.
Volga R.
Vyatka R.
Kama R.
West Dvina R.
Oka R.
Dnepr R.
Sura R.
Belaya R.
Pripyat' R.
Desna R.
Ural
Dnestr R.
Dnepr R.
Don R.
Emba R.
Volga R.
Kuban' R.
Kuma R.
Kura R.
200
0
200
400
600 km
1
2
3
4
5
6

the boundary turned steeply southwest. Passing through the city of Ishim it proceeded in the form of an irregular line in the same direction into the region south of Kurgan.

The southern boundary of this region of habitation of roe deer rose steeply north from the southern extremity of the Urals roughly up to the latitude of Troitsk on the eastern side of the forest zone of the range. From there it turned sharply east, passed through Troitsk, intersected Tobol, formed a projection southward along the right bank of the Tobol up to the latitude of Kustanai, and a similar projection from the region south of Kurgan to Kokchetav.[156]

Around this period of extreme contraction, a break in the range occurred along 55° N lat. for a distance of about 1,500 km or roughly 24° between the western point of distribution in the Urals and the eastern boundary of the western region (excluding the narrow projection in the Kharkov region and the section at Voronezh), which formerly represented a continuous range. The Ural-western Siberia distribution by then was also separated from the range covering the rest of Siberia; in the region of Omsk, Novosibirsk, and the Pri-Altai steppes roe deer likewise disappeared. The interruption of the range there was somewhat less than in the European part of the USSR. Precise data are few and while it is possible that the interruption of

---

[156] The boundary of Ural-western Siberia distribution is based mainly on data from Lavrov (1928), while that for Troitsk, Kustanai, Kurgan, and Kokchetav is based on unpublished data compiled by V.G. Heptner.

The outlines of individual occurrences given here and at some other places later are somewhat schematic and generalized. Some details are available in Lavrov's work (1929) and in faunistic studies of the 1920's and early 1930's.

---

191 Fig. 62. Geographic range of roe deer, *Capreolus capreolus* L. and its changes in the European part of the USSR and the Caucasus (scale in km).

1—boundary during utmost reduction of range by 1930 (mostly in the first half and middle, and partly at the end of the 1920's; this boundary in the Crimea and the Caucasus corresponds also to the boundary depicted in no. 3); 2—isolated pockets of occurrence of roe deer in the 1920's—Voronezh sanctuary, Novomoskovsk region, and Black Forest; 3—boundary of range at the time of its maximum enlargement in the mid-1950's; 4—northern and southern boundaries of the reconstructed range of roe deer where it does not coincide with the boundary for the mid-1950's; 5—some distant transgressions of roe deer after the 1930's—Balakhna, the mouth of the Kama, Volsk and Karelia Isthmus; 6—region of occurrence of roe deer of unidentified origin (partly acclimatized) in northern Moscow region. Question marks indicate probable habitats in the past (reconstructed range) along the Ural valley (same for Volga). V.G. Heptner.

192 the range in the west of the European part of the USSR and Crimean and Caucasian sections represents the result of processes occurring over a very long period, the eastward interruption in western Siberia arose quite recently, just before and during the 1920's.

The Siberian-Far East distribution of roe deer commenced in the west in the Altai. The range boundary encompassed this area in the form of an arc commencing at the boundary with China. It traversed somewhat north of Zaisan, proceeded northwest slightly away from Irtysh, and then turned northeast in the form of an arc somewhere east of Semipalatinsk. Passing south of Biisk it turned into Stalinsk and later into Krasnoyarsk. In the Krasonyarsk region the northern boundary did not cross the Sibirsk [Trans-Siberian] railway line. East of the Yenisey it proceeded roughly at the same latitude through Aginsk region, slightly north of Taishet, and left at the Angara, roughly at Bratsk. Farther away the boundary turned markedly southward and intersected the Lena at Zhigalov as well as the Kirenga roughly at the same latitude. Turning northeast from there the boundary line extended somewhat north of the northern extremity of Baikal. Inclining somewhat south it encompassed the southern part of the North Baikal highlands and the upper reaches of the rivers of the Patom highlands, intersected the Vitim considerably south of Bodaybo,[157] and ran toward the middle reaches of the Olekma. From there it turned south toward the Stanovoi range. The details of its position farther east are not clear. Evidently it proceeded along the southern slopes of the mountains, but it is possible that it lay slightly more to the north as described above (see the outline of reconstructed geographic range). In any case there are no significant differences.

The Middle Asiatic portion of the range in the period of utmost depletion differed from the one described above in that roe deer were evidently absent in the Zaisan depression and Alakul'sk basin; this part of the range was thus isolated from the Siberian-Far East part. Roe deer evidently did not go that far down along the Balkhash river system valleys (Ili and Karatal) and probably did not reach up to Balkhash. The animals did not penetrate the Chu-Ili mountains, at least they did not thrive that far north, nor did they emerge far into the plains along the Chu River. At Karatau also they evidently did not penetrate that far north.

Geographic range in the 1950's. The period of extreme depletion of population and reduction of the range commenced, as mentioned above, during the 1920's, more precisely from the first half of that decade. The position was essentially similar by 1930 and in the early years of that decade. Some efforts toward expansion and restoration of the range were begun in the 1920's (in the middle and latter half of that decade); measures for conservation were initiated here and there but proved ineffective in altering the overall pattern of depletion. This is true primarily of the European part of the country, the Urals, and western Siberia.

---

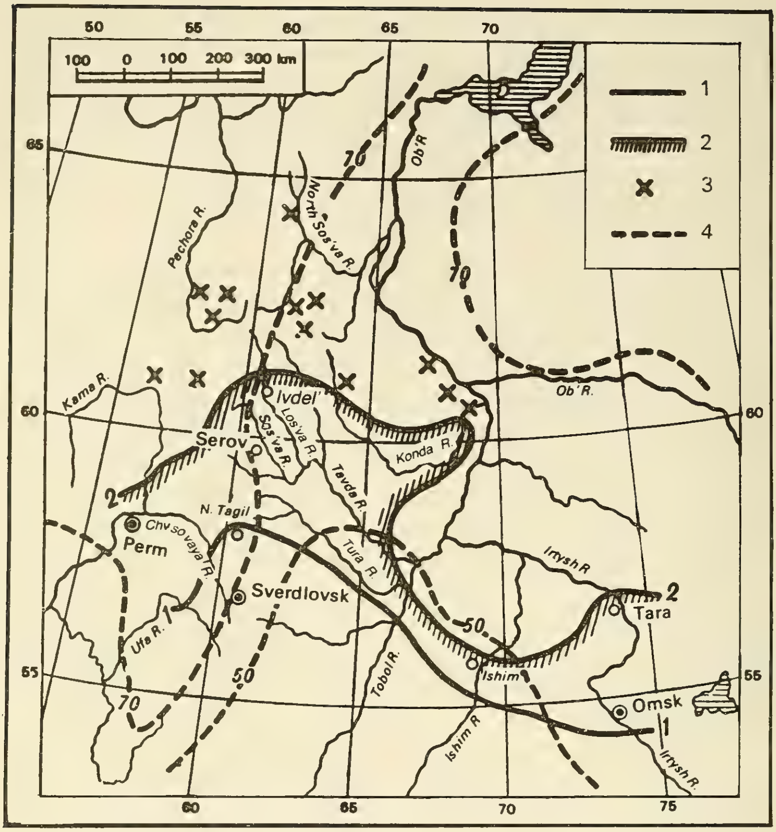
[157] The boundary up to the Yenisey is taken from the data of Lavrov (1929), and in Trans-Yenisey Siberia from Favorskii (1836).

Range expansion, leading to the present situation, became detectable in the 1930's. This process developed better in the 1940's. and continued intensely in the 1950's. The principle of expansion in various parts of the range is far from similar, however. In the European part of the USSR colonization in the western section has and is taking place in the east, partly in the south, in regions where the animal was formerly present, i.e., there is only a restoration of the range. It is proceeding extensively and quite intensely over a large territory, but is still far from realizing the former maximum range. The boundary has been restored only in a small section in the northwest. It has not been possible to identify the influence of any natural stimuli for colonization. The more important factors are undoubtedly lessened persecution by man and attempts at animal conservation (reacclimatization is not taken into consideration here; for this aspect see below).

In the Caucasian and Crimean parts of the range there are practically no settlements at all, and the position of the range in the last decade, to tell the truth, has not altered.

193 Colonization in the Urals, western Siberia, and Kazakhstan is proceeding intensely in all directions (see below). This also means the restoration of the former range, which has already reached its former maximum limits. In some parts there is even an enlargement of the range compared to its former boundaries. This process, occurring under the direct or indirect influence of man, is also associated with natural factors. One primary factor is the warming of the climate over a vast area. Thus, two processes have taken place in the past decade in the Urals and western Siberia and the outlines of the range given above for the zone under consideration represent more of the maximum than the reconstructed range (the latter term usually designates the maximum extent of the range in the past). As a result of colonization, mainly from the west, distribution in Ural-western Siberia has merged with the Siberian-Far East range.

194 At present in central Baikal, although some enlargement of the range has been observed, the former northern limit has not yet been reached. In Yakutia in the last decade and the last few years intense


50
55
60
65
70
100 0 100 200 300 km
65
60
55
1
2
3
4
Pechora R.
North Sos'va R.
Ob' R.
70
70
Kama R.
Ivdel'
Serov
Sos'va R.
Los'va R.
Konda R.
Ob' R.
Tavda R.
2
N. Tagil
Chusovaya R.
Perm
Tura R.
Irtysh R.
Sverdlovsk
2
Tara
Ufa R.
1
50
50
Tobol R.
Ishim
70
Omsk
1
Ishim R.
Irtysh R.
60
65
70
75

193 Fig. 63. Colonization of roe deer northward in heavy snow regions of the Urals and western Siberia (scale in km).

1—northern boundary of distribution in 1905 to 1915; 2—same in 1940 and 1941. Crosses represent northernmost points of transgression in the last decade (up to commencement of 1950's). Broken line indicates long-term mean height of snow cover in cm (from Nasimovich, 1955).

colonization has occurred and the range there now is much larger than the original range in the past, not only about a century ago but even in the 1930's and 1940's. It is in relation to this territory that there is utmost justification in referring to the range as maximum and not as reconstructed. The northward movement of roe deer there in the last decade was evidently the result of primarily natural causes. Farther away, in the east, i.e., in the region of the Stanovoi range and the Amur and Ussuri basins, colonization of roe deer has not occurred to any noticeable extent.

In the Middle Asiatic part of the range the process of enlargement has taken place but on a small scale in terms of area. Nevertheless, as a result of colonization from both sides, the Middle Asiatic and Siberian-Far East parts of the range merged. On the whole, the present range of roe deer is in a fluid state and a general tendency toward enlargement clearly manifested. However, the picture of range dynamics is not only complex but also different in different parts of the range. It is not determined everywhere by the same factors. In some parts these factors are purely man-made and in others natural or mostly natural, or a combination of both factors.

As a result of the phenomena described for the last decade the range has not only increased in size, but some restoration of its continuity achieved. By the middle of the 1950's it was broken down not into six but only into four parts: western, Crimean, Caucasian, and Siberian-Middle Asiatic, in which the Ural, Siberian-Far East and Middle Asiatic parts had merged. If this tendency persists, the merger of western and Siberian-Middle Asiatic regions can be expected in the future.

The range of roe deer by the mid-1950's can be described as follows. The eastern boundary of the western habitat, commencing on the southern bank of the Gulf of Finland encompassed Karelia Isthmus, going from there into Finland, proceeding farther along the southern bank of Lake Ladoga, and reaching roughly the mouth of the Syasa. From there the boundary line ran southeast into Tikhvin, then in the same direction into Rybinsk reservoir (Darvinov preserve), and into Yaroslav. In the section from the Gulf of Finland up to Yaroslav the range boundary has already been restored. Evidently associated with this part of the range are long excursions of roe deer as far as Balakhna northwest of Gorkii.

From Yaroslav the range boundary turned steeply southwest toward Pereslav-Zalessk and from there westward into the Zavidov region (on the southern bank of the Volga reservoir intersected by the line joining Moscow-Leningrad).[158] From here the boundary

---

[158] Roe deer have been encountered, though rarely, throughout northern, northwestern, and partly western parts of the Moscow district, in the regions of Konstantinov (north of Zagorsk), Dmitrov, Klin, Vysokov (west of Klin), Volokolam, Novopetrovsk (east of Volokolamsk) (Danilov, 1947) and Shakhov (west and southwest of Volokolamsk; L.P. Rasshivalina), and probably in some other regions.

It is possible that, at least partly, this was a part of the natural range formed as a result of colonization from the west and northwest. At the same time, however, there is no doubt that the Moscow portion of the range was formed to some extent by Siberian roe deer released time and again for purposes of acclimatization in the Zavidov region (those released in Pogonno-Losin Island in Moscow evidently per-line turned south, passing somewhere along the area between the 195 Moscow and Smolensk districts, possibly through northwestern region of Moscow district: Lotoshin, Shakhov, and Volokolam. Forming a broad arc it proceeded farther, evidently through the region west of Kaluga, Orel, or slightly west of it, and turned southeast to pass slightly north of Voronezh (Voronezh preserve) and, at the mouth of the Voronezh River, into the Don.[159] From there, the boundary line, for reasons not yet clear, proceeded east into the Khoper and encompassed the forest stretches in the river valley between Novokhopersk and Borisoglebsk and the lower reaches of the Vorona (Borisogleb forest, Tellermanov wood, and Khoper preserve). It is also possible that this section of the range was isolated.[160] Visitations of roe deer, evidently from the west, were observed during the war years even more to the east, in the region of Vol'sk.

From the Khoper, also in an inexplicable manner, the boundary proceeded southwest to Valuika and from there turned steeply southeast along the Derkul River, which flows into the Donets from the left near Lugansk, and proceeded toward a point slightly north of Belovod. Along the Derkul, the boundary ran up to its mouth where roe deer lived in Krasnoborsk forest. From there the boundary proceeded northwest into the Izyum region and slightly inclining southwest turned into the Novomoskovsk (northeast of Dnepropetrovsk), intersected the Dnieper, and evidently ran through the Kirovograd district to the Pervomai and Kotov regions,[161] then changed its westerly direction southwest and entered Moldavia. From Kotov it ran southwest to the Dnestr, descended along it to the south through

---

ished totally). i.e., formed artificially. It is, however, impossible to establish this at present since the taxonomy of Moscow roe deer has not been studied. There is only one partially identified reference that in Zavidov European roe deer coming independently from the west were also found along with imported Siberian roe deer (Danilov, 1947). The presence of European deer could also be expected in the Volokolam region and Shakhov, as also in Klin and Vysokov. The dubious occurrence of roe deer in northern Moscow region has been depicted by a hatched line in the map.

[159] Information about the range of roe deer from Voronezh up to the border of Moldavia is scanty and very generalized.

[160] These data pertain to the 1930's (Izmailov, 1940). At present roe deer are evidently absent in this section although they did exist there even in the 1940's (B.V. Obraztsov). Thus roe deer appear and disappear periodically in this peripheral point of the geographic range.

[161] It is possible that the boundary of a fairly uniform distribution ran slightly more north and encounters at Novomoskovsk and the Black Forest of Kirovograd region are isolated cases. There are references (Korneev, 1952; and others) to the effect that the Siberian and not the European form of roe deer inhabited these two points. Verification is required however.

Bendera to Kaushan and farther to Oloneshta, then turned southwest and going through Tarakliya ran across the Prut into Rumania. Thus the steppes of the Izmal' district do not form part of the range.[162]

The outline of the western part of the Siberian-Middle Asiatic distribution of roe deer changed very extensively by the mid-1950's, moving considerably westward, especially in the southern part, quite significantly southward, and very extensively northward. The western boundary of this section of the range commenced in the south, on the Ural River slightly below the mouth of the Ilek (at Nizhne-Ozernaya), proceeded northwest to Totskoe, passed to the west of Buzuluk somewhere between Buzuluk and Kuibyshev, ran farther to Buguruslan, encompassed Belebeev rise from the west, evidently turned slightly east, and exited at Menzelinsk slightly southwest of the mouth of the Beloe. There the new boundary joined the reconstructed and later even coincided with it, or almost so. From Menzelinsk the boundary bent east or northeast fairly sharply and, in a manner not yet clearly understood, proceeded north along the foothills of the Urals somewhere between 57 and 58° E long.[163]

The relatively small extension of the northern section of the western boundary into the west is explained by the very heavy snow in that section of the western Cis-Urals. There is essentially no possibility of further enlargement of the range into the west there, unlike in the south. The northward enlargement of the range of roe deer along the Urals has been very pronounced over the last decade.
196 The outline of the range there corresponds to that described earlier in discussing the reconstructed range. There is, however, justification to assume that colonization of roe deer in the northern section of this region does not represent exclusively the restoration of the range which existed sometimes in the past, but also the occupation of new territory in which roe deer were previously absent.

The southern boundary of this part of the range, commencing in the west in the Urals at the mouth of the Ilek, encompassed the Ilek basin together with Khobdo and proceeded farther through Kazakhstan as described in the depiction of the reconstructed range.

Visitations by roe deer to the mouth of the Kama are known from the area described here (V.A. Popov et al., 1954).

---

[162] The boundary line described is based on data from Kalela, 1948; Fedosov, 1951; Danilov 1947; Siivonen, 1953; Bobrinskii, 1944; Korneev, 1952; Nasimovich, 1955; Formozov, 1946; Elpat'evskii, Larina and Golikova, 1950; Izmailov, 1937; Kuznetsov, 1952; and others (including the unpublished data of B.V. Obraztsov, I.P. Rasshivalina, and V.G. Heptner).

[163] According to Kuklin, 1951; V.A. Popov et al., 1954; and the unpublished data of V.A. Popov and S.V. Kirikov.

The advance of the eastern boundary eastward in the western area inhabited by roe deer, and the western boundary westward of the Siberian-Middle Asiatic region, indicate an eventual merger of these regions into a continuous range. The break in the 1920's extending for about 1,500 km or 24° had shrunk to 900 km or 10° longitude at the narrowest section (between 50 and 55° N lat.) by the mid-1950's. Roe deer visitations from west to east and vice versa, reaching the Volga, support this possibility. If appropriate conservation measures are undertaken, the merger of these parts of the range is entirely probable since the natural conditions are quite conducive.[164]

The contemporary southern boundary of the Siberian-Middle Asiatic distribution of roe deer coincides with the reconstructed range described before and represents, as pointed out, the boundary of the Middle Asiatic part of the range. The latter also corresponds to the range described above.

The northern boundary of the range in Siberia and the Far East fully coincides with that of the reconstructed range all along its extent except for a small section beyond the Yenisey. There the boundary crosses the Yenisey slightly north of Krasnoyarsk, runs east roughly along 56°, intersects roughly at that latitude the upper courses of the Biryusa and Chuna, descends in the form of a promontory in the interfluve of the Chuna and Angara toward the south almost up to 55°, again rises in the north along the left bank of the Angara, and turning east crosses it at the mouth of the Ilim. From there it again turns south and, crossing the Lena at Zhigalov and the Kirenga almost at 55°, again runs north encompassing from the west the Northern Baikal and Patom highlands, crosses the Lena, and becomes the reconstructed boundary on the left bank of Lena in the Nyuya basin as described earlier. Thus, the present-day boundary lies somewhat south of the reconstructed one described above.[165]

As mentioned before, at some places in the region north of Baikal, especially in Yakutia, colonization of roe deer beyond the limits of the former range took place in the last decade. It should be emphasized that here the process proceeded extremely intensely, evidently more intensely than in other parts of the range. Judging from all available information the effect of natural causes was particularly important although the human factor (reduction of persecution) was not negligible. All information relating to the last century, commencing from Maak (1859), points to the distribution of roe deer as a rare phenomenon in the north, only up to the mouth of the Vitim. One transgression was recorded on the Vilyuya toward Suntar in the region south of the southern bend of the Vilyuya. Slightly more eastward deer were distributed along the Olekma. This was the situation until the last decade. According to information even for the 1920's, 1930's, and partly 1940's the northern boundary of roe deer usually traversed south of the Northern Baikal highlands to the south of Bodaibo, and beyond in the lower reaches of the Chara and Olekma, and still farther into the passes in the Patom highlands from the south. Some data point to their occurrence along the Lena above the mouth of the Olekma. In other words, Yakutia along the left bank of Lena, and along the right bank east of the mouth of the Olekma was not inhabited by roe deer.

---

[164] A merger of the Caucasian and, even less, the Crimean part of the range with the northern should not be anticipated.

[165] According to the data of Favorskii, 1936; Podarevskii, 1936; Kopylov, 1948 and 1950; Fetisov, 1953; and other sources. Also see footnote no. 142.

197 An extremely intense colonization of roe deer took place in northern Yakutia in the 1940's and 1950's. During that period almost all the region between the Lena and the middle and southern Vilyuya was completely occupied by roe deer, which even crossed the northern Vilyuya. Colonization of roe deer in the region between the Lena and Amga, i.e., east of the Lena, commenced very recently, in 1953 and 1954 (D.U. Ivanov).[166]

Colonization of roe deer in Yakutia continues and a further enlargement of the range there, especially north of the Vilyuya, can be expected. It is significant that roe deer occupied the area in Yakutia first along the Vilyuya and also along the Lena and the lower reaches of the Amga, all of which regions represent zones with natural topographies of steppes and forest-steppe types. The thinning of forests in that part of the country was also favorable for these animals. It is significant that at some places in the newly colonized localities, for example around Yakutsk, roe deer prospered into fairly large populations (D.U. Ivanov).

The present-day range of roe deer in the Crimea, as in the 1920's, is confined only to forest zones in the mountains of the peninsula.

The range of roe deer in the Caucasus has not undergone marked variations since the time of maximum contraction, and whatever changes occurred at some places were insignificant. This is explained by the occupation of roe deer, even in the 1920's, of almost all the area favorable for their survival, i.e., the forest zone of the Caucasus.

---

[166] Some published maps of geographic ranges (Bobrinskii, 1944) in which the northern boundary along the right bank of the Lena runs from the Olekma in the form of an arc toward Uda Bay, terminating on the Aldan beyond 60° N long., do not at all represent the prevailing state in that period and were incorrect even for 1955 and 1956.

The complex outlines of the range of deer in the Caucasus are connected with the forests. Commencing in the west around Novorossiisk, it extends in a belt along the forest zone of the northern foothills and the middle montane belt right up to Caspian Sea, running toward it in the area south from Makhachkala to Divicha (around 41°10′ N lat.). This band is extremely variable, depending on the width of the forest zone; in the west it is broad and reaches toward northern Maikop and Nal'chik; it is very narrow in the central part of the mountains and reaches only up to Vladikavkaz; it broadens again slightly in the east. Roe deer are absent in the whole of the high mountain region and in the forestless zones deep in the mountains, for example, in many regions of Dagestan.

Along the southern slope of the mountains the range of roe deer extends in a very narrow band from the region of the source of the Pirsagat (north of Shemakha) up to Tbilisi and farther west. The range covers essentially the whole of the western Trans-Caucasus and extends in a narrow band along the southern slope of the Glavnoi range to the Sochi region where it joins the north Caucasian part of the range. All the steppe zone of eastern Trans-Caucasus up to Tbilisi inclusive is devoid of roe deer. They are also absent slightly west of Tbilisi along the Kur'.

In the rest of the Trans-Caucasus the range is in the form of a narrow band running from the western Trans-Caucasus in the south, east toward southern Tbilisi, passing north of [Lake] Sevan and running farther southeast to Araksa. This band includes the mountain ranges of Papakar, Pambak, Shakhdag, Murov-Dag, and Karabakh. In the Zangezur mountains roe deer are evidently absent but their range includes the Kafan and Megra regions, associated with the Bargushat mountains, and the eastern slopes in the southern parts of Zangezur. Toward Araksa this projection of the range thus runs in the region between the Megra (southernmost point in the bend of the river) and the Karyagin region.

In Armenia the southern boundary of this projection runs through Stepanovan and Kirovakan regions on the western margin of Sevan. North of Sevan this section of the range is very narrow and falls far short of the railroad and Kirovobad. In the region south of Tbilisi its eastern boundary extends approximately to Shamlug, running west of the railroad to Shamlug.

The bottomland deciduous forests of the lower Terek in the zone

198 slightly above Kizlyar and below the mouth of the Sunzha represent an altogether different section of habitation of roe deer in the Caucasus. Evidently roe deer are also encountered in the lower reaches of the Sulaka north of the railroad (Vereshchagin, 1947; map), where they were absent in the 1920's (V.G. Heptner). Another isolated section is the forest zone of Talysh, which represents an independent projection of the Iranian-southern Caspian part of the range of the species.[167]

In the last decade roe deer, mainly Siberian and Far East animals were transplanted at several places beyond the prevailing range: in Zavidov on the line connecting Moscow-Leningrad, on the southern bank of the Volga reservoir northwest of Klin (successful colonies, see above), on Pogonno-Losin Island near Moscow (this settlement was evidently unsuccessful), and in Prioka-Terras preserve near Serpukhov (successful). In the 1950's especially in the later half of this period, roe deer, mostly eastern forms (Siberian, Tien Shan, and Far East), have been colonized time and again at many places by game organizations. Sufficient information about these efforts is not available and in several cases the results are altogether unknown. These have therefore not been discussed here.

Geographic Range outside the Soviet Union

The range outside the Soviet Union (reconstructed) covered all of western Europe and in the south up to the Mediterranean Sea and Sicily inclusive (absent on other islands). In the west the range covered England but not Ireland, and evidently never existed there. The northern boundary in the Scandinavian peninsula (including Finland) commenced on the Atlantic coast around 65° N lat., descended south, encircling the main axis of the Scandinavian mountains roughly up to 62°30′ to 63°, and rose far north along the Pri-Baltic region of Sweden in the form of a band reaching the arctic circle (the northernmost point of habitation of the species). From there it descended steeply south and, traversing roughly along the eastern boundary of Finland, ran along the west coast of Lake Ladoga and the Karelian Isthmus.[168]

---

[167] The range of roe deer in the Caucasus is based on data from Vereshchagin, 1947; Dal', 1954; Heptner and Formozov, 1941; and others (including original data of V.G. Heptner).

[168] The range boundary in Scandinavia is taken from Ekman, 1922; Kalela, 1948; and Siivonen, 1953. Roe deer regularly inhabited Sweden north only to approxi-

In the east the range covered Asia Minor, northern part of the Syrian zone of the United Arab Republic, northern Iraq and Palestine up to Lake Genisaret (Tiberius), and Haifa (Mount Carmel) and Iran. The range boundary in these countries to the south is not clearly understood. Evidently it extended in a narrow belt along the Elbruz and the adjoining forests of the southern Caspian district ("Hyrcania"). In the east the range apparently penetrated up to the meridian of the southeastern corner of the Caspian Sea, but did not reach the Atrek basin. Roe deer were absent in the rest of Iran and in Afghanistan.

In central and eastern Asia the range of roe deer included the eastern half of the Tien Shan, but the limits of their distribution in the east, in this part of China, are not clearly known. In Mongolia the range encompassed the Mongolian Altai roughly up to 92° E long., spurs of the Altai to the west of Lake Ubsu-Nur, Khan-Khukhei mountain to the northeast of Lake Khirgis-Nur, montane country of the Khangai in the south roughly to 46°, Khentei in the south to Ulan-Bator and almost 47° N lat., and approximately to 115° E long. in the east (Bannikov, 1954). The Mongolian zone of habitation of the species led directly almost everywhere into the range within the USSR.

Farther away in the east the range included a considerable part of the eastern half of China. The western boundary of this part of the
199 range extended from west of the Great Khingan, including its spurs, to south of Lake Buir-Nur within the Mongolian Republic, and from the southern extremity of the Khingans, passing to the west of Peking, ran toward the Hwang Ho and the northeastern corner of its great northern bend. From there the range extended as a narrow projection into the west along the Inshan mountains lying north of the longitudinal course of the river. From the eastern extremity of

mately 64° N lat. and the southeastern corner of Norway. The rest of the area represented zones of fairly frequent or rare visits. In northern and northwestern Finland roe deer evidently originated from Sweden, and in southeastern and southern Finland from the USSR, mainly through Karelian Isthmus (migration through Svir dubious, V.H.). In Scandinavia in the present century intense colonization of roe deer in the north has occurred, especially in the last decade. The maximum contraction of the range took place at the end of the last century when roe deer occurred only in the extreme southern part of Sweden. In 1955 and 1956 they spread, as mentioned before, and not only reached their one-time maximum range, but at some places in the USSR even exceeded it.

the Inshan the boundary initially descended south and later ran west, bypassing the Ordos desert (within the arc of Hwang Ho) on the south. West of the Hwang Ho (that section running north) the range extended in the form of a narrow projection along the river to the north of the Ala Shan mountains. It also ran slightly west, occupying the eastern part of the Nan Shan range. Passing to the east of [Lake] Koko Nor the boundary turned south, including in the range eastern Tibet (regions of upper Hwang Ho, Yangtze, and Mekong) and the Kam country (Flerov, 1952). From there it became the southern boundary of the range, ran through northern Szechwan, and covered southern Shensi and Shansi, approximately to the region of the Hwang Ho estuary.

The range in China, namely in eastern and southeastern China, evidently changed very extensively long ago. It is highly probable that at some time in the past it extended to the Yangtze and occupied the entire country between this river and the Hwang Ho. At present it is possible that roe deer inhabit the region in the northern bend region along the midcourse of the Yangtze.

All of the Korean Peninsula and Cheju-Do Island fall within the range.

Fossil remains of roe deer are known only from within the present-day range or at its boundaries (Syria—Pidoplichko, 1951; Kondopoga and right bank of the Svir—Kalela, 1948). (V.H.)

Geographic Variation

The magnitude of geographic variation in the species is significant from a purely morphological point of view, i.e., with reference to sharp differences between extreme forms. However, the number of races, considering the vastness of the range, is comparatively moderate and in any event much smaller than the number of names assigned to the species (see the synonyms). At the same time, in some limited areas, especially in western Europe, roe deer tend to show local features, mainly in size and weight, as a result of local ecological conditions, primarily food situation, population density, etc. There is no justification for considering these variations as factors dividing the species into subspecies. Some variations in this genus were even recorded here years back (differences between roe deer of western and eastern parts of the Great Caucasus; Dinnik, 1910). Such forms have generally not been recognized as subspecies and only prominent races are acknowledged in Soviet literature. At the same time geographic variability in species cannot be considered clearly understood since their range is obviously somewhat oversimplified in the latest reviews (Ellerman and Morrison-Scott, 1951; Flerov, 1952).[169]

In the USSR races of roe deer fall quite naturally into two distinct groups—European and Siberian.

European Group

1. European roe deer, *C. c. capreolus* Linnaeus, 1758 (syn. *vulgaris, caprea, europaeus, transsylvanicus, balticus, albicus, warthae, armenius,* and *zedlitzi*). Small forms. Body length 100 to 136 cm, tail length 2.0 to 3.5 cm, height at shoulders 75.0 to 91.5 cm, maximum skull length 190 to 216 mm, and weight 20 to 37 kg[170] (Flerov, 1952; Sablina, 1956; Serzhanin, 1956).

200 Winter coat grayish-brown, darker in rear part of trunk and much lighter on sides. Summer coat generally brownish-rusty or rusty. Top of head grayish or brownish, differing from color of trunk. Young animals rust-colored with bright spots arranged mainly in three rows. Spots in uppermost row sharper and brighter than the rest. Tympanic bulla very small, set deep in auditory region, projecting weakly above articular process (Flerov, 1952). Antlers poorly developed and characteristic of European type.

Found in the European part of the USSR, including Belorussia, the Ukraine, Crimea, and Trans-Caucasus. Outside the USSR occurs throughout Europe, including the Balkans, Asia Minor, Iraq, Palestine, and Iran.

Until quite recently, as partly revealed by synonyms, several subspecies were recognized in this territory. The description of the nominal form was published only recently (Ellerman and Morrison-Scott, 1951; Flerov, 1952). Although it reflects the prevailing state better than the former approach, it is nevertheless somewhat simplified. Thus it is doubtful if Trans-Caucasian and Iraqi roe deer are identical with southern Swedish, central European, and Belorussian animals. This subject requires special study. The name *armenius* Blackler, 1916 should perhaps be assigned to the trans-Caucasian form.

---

[169] Voluminous data on geographic variability of characteristics (mainly meristic) of roe deer have been given by Pasternak (1956); Unfortunately this information has not been thoroughly studied. Pasternak's findings differ somewhat from those given here.

[170] The weight of 41 kg mentioned by Flerov (1952) evidently refers to a rare find. Latvian roe deer weigh on the average about 23 kg (Kalnin'sh, 1950) and German males 15 kg (Hempel et al., 1956).

Siberian Group

2. Siberian roe deer, *C. c. pygargus* Pallas, 1777. Largest form, attaining maximum size and found in the Urals, Pri-Baikal, and especially in the Altai-Sayan region. Body length of males 123 to 151 cm (M 134) and females 119 to 147 cm (M 129), height of males at shoulders 84.5 to 100 cm (M 90) and of females 80 to 96 cm (M 87.5), and height of males at sacrum 89 to 106 cm (M 98) and of females 87 to 105 cm (M 96) (Pri-Baikal; Fetisov, 1953). Maximum skull length 215 to 253 mm. Weight of males generally reaches 59 kg (Flerov, 1952) and of females up to 52 kg (Fetisov, 1953).[171] These animals are the largest of all the forms and possess the largest antlers in absolute as well as relative terms.

Winter coat in general brownish or bluish. Speculum large and white. Summer color rusty or rusty-red without contrast between coloration of head, trunk, and neck. Spots well defined in young and arranged in four longitudinal rows with additional groups of spots occurring on shoulder or/and thigh. Spots in upper rows do not differ from lower ones in brightness. Skull in orbital region relatively slightly narrower than in European forms. Tympanic bulla large, swollen, and projects prominently in auditory region (Flerov, 1952). Antlers in fully developed form, typical of Siberian type (see above).

These animals occur in the eastern half of the European part of the USSR, the Urals, and Siberia up to the Amur. Outside the USSR they are known in northern Mongolia.

It is very possible that roe deer are not taxonomically identical throughout the vast expanse from the Volga to Trans-Baikal.

The range boundary of Siberian roe deer is quite vague in comparison to the European since the roe deer is now extinct in all regions through which the [common] boundary once traversed. Evidently Siberian roe deer reached the Volga, occurring along its right bank, especially in the lower reaches of the Don (they lived in the town of Sarkel in the twelfth century; N.K. Vereshchagin). The boundary evidently did not run farther west of the Volga and much of the plains between the Volga and Dnieper were occupied by the European form, which is established there even today.

Reports that Siberian roe deer were encountered much farther
201 west, at least in the historic past, are apparently erroneous and based on some individual animals with particularly large antlers found among European roe deer even in western Europe.

---

[171] Average body length of Altai-Sayan animals according to Pasternak (1955) 140.4 cm; mean weight 35 kg.

Many reports exist that Siberian roe deer also lived on the right bank of the Dnieper in the Black Forest in Kirovograd region and on the left bank of the river in Samar forest in Novomoskovsk and Dnepropetrovsk regions (Brauner, 1915; Migulin, 1927 and 1929; Charlemagne, 1937; Korneev, 1952). Some regard this form there as a relict of the glacial period (Charlemagne, 1937), while others (Migulin, 1927 and 1929) concede transgressions into these places of Siberian or Caucasian animals. The subject requires special study, including a study of their systematics, but it is extremely doubtful if true Siberian roe deer lived in these places. This is particularly contraindicated by the occurrence of the European form in Crimea. Finds of remains of Siberian-type roe deer in Orlov region (Gorbachev, 1915; Flerov, 1952) pertain evidently to extremely ancient periods.

The foregoing discussion points up the near impossibility of delineating the range boundaries of both these forms between 30 and 35°E long. (Flerov, 1952) over the historic period. It is entirely possible that in the Quaternary period in the west, even in western Europe, roe deer of Siberian type did exist and that the western form represented a younger generation produced by diminution. However, geographic relations over the historic period were probably the same as discussed above.

At present it is nearly impossible to study the subject of former range boundaries since Siberian roe deer are not established west of the Volga, while the European type has noticeably advanced eastward. Moreover, Siberian and Far East animals were introduced by man in the Moscow district and some other regions and the picture has been greatly confused.

3. Tien Shan roe deer, *C. c. tianschanicus* Satunin, 1906 (syn. *ferganicus*). Very similar to Siberian form in color but slightly smaller. Maximum skull length 218 to 238 mm (M 226). Features of similarity in the skull structure with the Caucasian form also evident (Pasternak, 1955). Antlers large.

Found in Tien Shan. Outside the USSR they occur in Chinese sector of Tien Shan.

The type is not well known and the form within the Soviet Union has not been studied. Some authors place Tien Shan roe deer among Siberian forms but this is extremely dubious.

4. Far East (Manchurian) roe deer, *C. c. bedfordi* Thomas, 1908 (syn. *mantschuricus* and *ochracea*). Very similar in structure to Siberian roe deer, from which it differs in slightly smaller overall size and smaller antlers. Body length averages about 122 cm and weight about 28 kg (Pasternak, 1955). Maximum skull length 211 to 236

mm and average 226 mm. Winter coat ocherous-rusty or gray with a rusty tinge. Speculum with faint rusty tinge. Summer coat bright rusty and full, more so than in Siberian form.

Found in Ussuri region and Pri-Amur. Outside the USSR this form occurs in northeastern China and Korea.

The range boundary of Far East roe deer in comparison with the Siberian form is not clear. Evidently roe deer of Great Khingan in the east, in expanses adjoining the Amur from the north and possibly in the Amur itself, possess transitional features from the Siberian form. In the most typical form this subspecies is found in China and the southern Ussuri region in USSR (Primor'e territory).[172] Thus, the northern range boundary of the subspecies and the region of its merger with the Siberian form fall in the USSR.

202 5. North Caucasian roe deer, *C. c. caucasicus* Dinnik, 1910. Size moderate, intermediate between European and Siberian roe deer. North Caucasian roe deer are fairly large and have antlers of the Siberian type. Body length reaches up to 1.5 m with an average of roughly 130 cm. Weight does not exceed 40 kg and heavy animals are very rare; average weight about 30 kg. Maximum skull length 216 to 235 mm (M 225). Antlers not more than 33 cm in length.

Found on the northern slopes of the Great Caucasian range from Novorossiisk and Sochi to the Caspian Sea coast and from the mouth of the Terek to Derbent. Does not occur outside the USSR.

North Caucasian roe deer have been studied very little and their features are inadequately defined. Nevertheless, there is no justification for denying their independent existence and placing them among the true Siberian form (*C. c. pygargus*; Flerov, 1952). In general the North Caucasian form is smaller than the Ural and other Siberian roe deer.

Trans-Caucasian (*C. c. capreolus*) and North Caucasian forms are found together at some places (western extremity of the geographic range, Dagestan, lower course of the Terek). Trans-Caucasian type animals, which cannot be distinguished from them, are also found within the range of North Caucasian forms. Apparently some show transgression of particular characters in both directions. There is no doubt of a fairly extensive hybridization of both forms. These relations have not been accurately delineated. It is possible that the race under description is generally of a hybrid character formed as a result of the encounter between two strains of Caucasian populations of roe deer, i.e., Siberian from the north and European from Asia Minor into Trans-Caucasus. In addition to these differences, the North Caucasian form also differs distinctly from the Trans-Caucasian in skull measurements (skull length of roe deer from the latter area 184 to 213 mm—M 200) (Pasternak, 1955).

---

[172] Farther south, in the central and southern provinces of China and eastern Tibet, some authors acknowledge the existence of one more form of Siberian type close to the Far East type, i.e., *C. c. melanotis* Miller. Others consider this form identical to *C. c. bedfordi*. The latter view appears more correct.

The presence in northern Caucasus of Siberian-type roe deer serves as yet one more proof of the former occurrence of Siberian roe deer on the right bank of the Volga and along the lower Don.

Outside the USSR, apart from the forms discussed above, yet another form occurs—*C. c. melanotis* Mill., 1911 (northeast Tibet, Kansu, and Szechwan). It is proximate to the form *bedfordi* and possibly the two are identical. (V.H.)

Biology

Population. According to rough computations of data for the 1920's the average population density of roe deer in the forest areas of the USSR was 0.67 per 1,000 hectares (Lavrov, 1929). In the last few decades the range of roe deer has expanded and the animals have penetrated farther north into Siberian and Kazakhstan forest-steppes (see above) and multiplied.

In the last decade roe deer were most numerous in eastern Siberia, in the southern Far East, at some places in Kazakhstan forest-steppes, in the Altai, and Trans-Urals. In eastern Siberia roe deer were especially numerous in the southern Irkutsk and Chita regions and in Buryat and Tuvin Autonomous regions. Here their populations rose in some places up to 25 to 50 animals per 1,000 hectares (Timofeev, 1949; Kopylov, 1950; Fetisov, 1953; and others). In the Far East roe deer were most numerous in the Jewish autonomous and Amur districts (Adramov, 1954). In the Altai they were particularly numerous in the Gorno-Altai Autonomous Region, especially in Ust-Kan, Ust-Koksin, Shebalino, and some other regions. In Il'men preserve, from the end of the 1930's to the early 1940's, over an area of about 50,000 hectares there were usually 1,200 to 1,500 roe deer in winter, which in the exceptionally snowy winter of 1940 to 1941 rose to 3,500 (Ushkov, 1954).

In the European part of the USSR roe deer are a common sight in the Baltics (mostly in Lithuania and Latvia), Belovezh Forest, Crimea, and at places in the Caucasus. In Latvia up to 34,000 roe deer were counted in 1939 but their number decreased in the years following the Great Fatherland War and the population was restored later: 203 8,500 animals in 1948; 15,500 in 1955; and 17,880 in 1957 (Ivanauskas, 1957).

In Crimean preserve 1,300 roe deer were counted in 1950, or an average of about 40 animals per 1,000 hectares in the area in which the animals lived. Outside the preserve in Crimea the population touched 3,300 animals, with the density being highest in the Alushtin region (35 per 1,000 hectares), Staro-Crimea (28), Bakchisarai (20), etc. (P.A. Yanushko). In the early 1920's there were about 5,000 roe deer in Belovezh Forest (Severtsov, 1940; and others). Later, the population there decreased to about 500 by the end of the 1940's (by that time the area of the Forest was also reduced); in some individual woods density varied from 1 to 18 animals per 1,000 hectares (Sablina). In the Ukraine and Belorussia on the whole, as also in the central regions of the European part of the USSR, roe deer were few.[173]

In the mid-1800's the population of roe deer was markedly high almost everywhere. It was exceptionally so in the Urals, southern Siberia, and the Far East, where herds of several hundred animals were sighted during seasonal migrations (Sabaneev, 1875; Nasimovich, 1955).

Habitat. Roe deer inhabit regions with diverse climates, from humid marine to dry continental. They inhabit forest-steppe sections and diverse types of deciduous, mixed, and coniferous forests, as well as tugais, thickets of reeds or rushes along the periphery of steppes, and sometimes areas around semidesert lakes. When rational game management is practiced, they survive well in cultivated places and densely populated areas. In the snowfree period of the year the vertical range of dispersal is quite extensive, from sea coasts to subalpine and lower alpine meadows; in the Urals and Trans-Baikal up to 1,000 to 1,500 m (mountain-steppe meadows and balds); in the Caucasus and Altai up to 2,000 m; and in the Tien Shan mountains up to 2,800 to 3,300 m. They prefer smooth areas in the mountains and are more common in rugged localities in the plains and foothills. They prefer light forests with abundant young deciduous trees and undergrowth alternating with glades, clearings, and meadows; they avoid dense boreal forests of the taiga type. The extensive penetration of roe deer into the taiga zone in the last decade was facilitated by the felling of dense coniferous bottomland forests and the creation of burned-over forests with reseeded deciduous tree species (Skalon, 1946; and others). In the past roe deer of the forest-steppes penetrated far into the open steppes and even today are seen at some places in western Siberia and Trans-Baikal under similar conditions, but in very small numbers.

---

[173] In cultivated lands, especially when the population of competing species is low, the population density of roe deer can run very high; for example, in Bavaria it averages 84 per 1,000 hectares (Grushvits, (1957).*

*Not in Literature Cited—Sci. Ed.

The preference of roe deer for a given type of habitat varies widely in different sections of the geographic range. For example, in Belovezh Forest roe deer are particularly numerous in mixed pine-oak-spruce forests, among pine undergrowth, and in oak-hornbeam and beech forests; roe deer also visit marshes (Sablina, 1955; Serzhanin, 1955). In Lithuania roe deer inhabit forests of all types and composition but are mostly confined to mixed forests with well-developed young trees, burned-over forests, and clearings; they are scarce in spruce and even scarcer in pine groves (Kuznetsov, 1954). In the Caucasus, although roe deer are encountered in summer right up to subalpine meadows, they are most numerous in broad-leaved forest sections with young deciduous varieties of trees and large clearings covered with dense herbaceous vegetation seeded by man (Dinnik, 1910; Nasimovich, 1939). Beech forests with tall trunks and numerous young trees represent one of the favorite summer habitats of roe deer in Crimea (Lavrov, 1929; Dal', 1930). In the Urals and western Siberia roe deer prefer mixed pine-birch forests with aspen groves, 10-year-old burned-over forest sections and clearings, and are
204 attracted to plantations adjoining glades and marshes, common in the floodplains of rivers. In the steppes they are confined to forest islets and reed thickets along the banks of lakes (Sabaneev, 1875; Vinitskii, 1937; Averin, 1949; Kurazhskovskii, 1949; Yanushevich and Blagoveshchenskii, 1952; I.P. Laptev, 1958).

In the Altai, eastern Siberia, and along the Amur roe deer are particularly numerous in deciduous (at places also pine) forests with dense deciduous undergrowth of shrubs and grasses, in regenerating burned-over forests, in tiny birch-aspen groves adjoining cultivated fields, meadows, and steppes (Altai, the Sayans, and Trans-Baikal). Roe deer avidly feed in sedge-clover marshes,* sorghum fields (Altai), open ridges, and burned-over forests. They seek refuge in boreal forests, shrubbery thickets along river banks, etc. (Cherkasov, 1884; Dmitriev, 1938; Nasimovich, 1949; Pavlov, 1949; Timofeev, 1949; Kopylov, 1950; Fetisov, 1953). In the Far East roe deer are confined to sparse deciduous and burned-over forests; they penetrate deep into the Sikhote-Alin only along river valleys and avoid coniferous forests (Kaplanov, 1948; and others).

The habitats of roe deer are extremely diverse in Middle Asia, where this species is common in spruce forests (central, northern, and eastern Tien Shan), often encountered in fruit- and nut-bearing forests in midmontane altitudes, juniper forests, along tugais in rushes close to water sources, etc. In summer roe deer are most numerous in the subalpine belt of the mountains of central and eastern Tien Shan, where areas of spruce alternate with shrub thickets and tall grass meadows; the animals ascend to alpine meadows during early morning hours (Shnitnikov, 1936; Vakulenko-Snigirevskaya, 1940; Antipin, 1941; Kuznetsov, 1948; Shul'pin, 1948; Pasternak, 1955; and others). In the Tersk Alatau roe deer are found even in winter at heights of up to 3,200 m (R.P. Zimina).

---

*Not clear; may mean three-leaf sedge marsh—Sci. Ed.

Food. In the Soviet Union the food of roe deer has been best studied in Il'men preserve (Trans-Urals) (Averin, 1949), Irkutsk region, Trans-Baikal (Fetisov, 1947 and 1953), Belovezh Forest (Sablina, 1955; Pasternak, 1955), Crimea (Lavrov, 1929; Dal', 1930; P.A. Yanushko), and the Baltics. Observations are too inadequate in other regions to draw justifiable conclusions. Two relatively important food components for roe deer are herbaceous and tree and shrub vegetation; their relative importance varies according to topographic-geographic characteristics of a zone and its natural features. For example, in the Crimea, throughout the year including even summer, tree and shrub vegetation is of utmost importance in the diet of roe deer, while herbaceous and bulbous plants are important in other steppes and semideserts, and twigs in winter.

Usually leaves and green shoots of tree and shrub vegetation are consumed in summer and in winter shoots, branches, buds, and dry leaves (especially of aspen), and coniferous needles (most often of young pine, later juniper, and very rarely larch, spruce, or fir; needles of nut pines are not eaten). Tree bark is not usually touched and roe deer differ significantly in this respect from red deer and elk. In some regions (Belovezh Forest and Bashkir preserve) the importance of twigs in the diet of roe deer is more than in the diet of red deer (P.F. Kaznevskii). Among herbaceous vegetation roe deer consume avidly tips of shoots, racemes, and sometimes syncarps [infructescences] (western Siberia; Kurazhskovskii, 1952); in winter green parts and twigs projecting above the snow cover are also eaten. Blackberry, mistletoe (in forest clearances), winter horsetail, ivy, mountain oats (in northern Caucasus), and some other food plants are very important among winter-green plants.

On the whole roe deer of the Soviet Union consume up to 250 species of plants.[174] In Crimean preserve the consumption of 145
205 species of plants has been established (100 species of herbaceous

---

[174] According to Danilov (1958) roe deer consume about 174 genera of angiosperms alone (41 tree and shrub genera and 133 herbs).

plants, 29 tree and shrub, 4 lichens, etc.); of these, over 100 species are consumed in summer (including 63 which are eaten more often) and in winter 41 (and 14) (P.A. Yanushko). In the Irkutsk region and Trans-Baikal roe deer consume no less than 130 species (including 85 eaten more often) (Fetisov, 1953). In Il'men preserve 110 plant species are consumed by roe deer; of these, in spring 90, in summer 83, and in autumn and winter 64 or 65. Of primary or secondary importance are 24 plant species in spring, 34 in summer, 28 in autumn, and 15 in winter (Averin, 1949). In Belovezh Forest roe deer consume over 90 species (of which roughly 70% are herbs). In summer, compared with winter, food composition is far more diversified (Pasternak, 1955; Sablina, 1955). Plants serving as food for roe deer in the Altai include about 60 species (Pasternak, 1955).

Among tree and shrub foods preferred by roe deer and which usually play an important role in their diet are aspen, ivy, birch, linden, mountain ash, oak, ash, some maples, hornbeam (in the European part of the USSR), hazel nut, raspberry, etc. Several species, mainly because of their extremely limited availability, are important only in small parts of the geographic range, for example, dogwood and jasmine in the Crimea and the Caucasus, smoke tree in the Crimea, Daurian rhododendron in Trans-Baikal, and lespedeza, Amur vine, actinidia, etc. in Primor'e. At places where the population of roe deer or tree-eating ungulates is high and preferred foods inadequate, roe deer consume large amounts of pine needles in winter (Il'men preserve, Belovezh Forest, Baltics, etc.). Pine needles are usually most intensely consumed in the latter half of winter when the height of the snow cover is considerable (Averin, 1949). Thus pine food may serve as a fairly reliable index of winter food availability for this species. The same can be said of spruce with even greater justification; spruce is usually consumed only when the population density is extremely high, as observed in the Baltics.[175]

Among herbaceous plants of great importance in spring are umbellifers (cow parsnip, angelica, and chervil), composites (yarrow, hawkweed, and crepis), legumes (pea vine, vetch, and clover), buttercups (double buttercup, crowfoot, and anemone)—and in early summer, sedges and grasses (new growth is consumed avidly, as is old). Avidly consumed species also include some gentians, especially buckbean, in search of which roe deer often visit marshes, geranium, bistort, St. John's wort, burnet, and in southern Siberia lilies (bulbs of *Allium,* martagon, and yellow lily), etc.; in spring pasque flower *(Pulsatilla patens), Scilla,* lungwort, primula, and others are also eaten well. Many plant species consumed by roe deer in large quantities are deleterious to cattle.[176]

---

[175] However, in the Naryn region of Alma-Ata district where roe deer are few, they quite frequently consume spruce needles in winter; in one case these needles constituted up to 50% of the stomach contents (Zhirnov, 1958).

Roe deer avidly consume fungi (armillaria, pepper mushroom, brown mushroom, chanterelle, and others), but these are not significant in their diet. In winter arboreal lichens (five to seven species) are often consumed avidly. In many regions acorns,[177] fruits of beech and other fruit-bearing trees (wild pear, apple, and others) serve as important food; birch catkins and many berries (mountain cranberry, blueberry, bilberry, cloudberry, bearberry, etc.) are consumed avidly. Fruits of nut pines, chestnut, sea buckthorn, and "birch lips" are also eaten (Cherkasov, 1884).

In winter, when necessary, roe deer can dig up twigs, etc. and acorns from under snow 10 to 15 cm deep. Instances are known of their digging up aspen leaves from under snow 1.5 m deep. Instances are also known of roe deer digging up and consuming fallen larch
206 needles (Trans-Baikal). In their diet selection roe deer are more adaptable than red deer in some regions (Yanushevich, 1950; Sablina, 1955), and inferior to the latter in other zones.

In most regions roe deer move well to natural and artificial salt licks. In Primor'e territory they emerge on the sea coast in search of aquatic algae and other marine products covered with salt (Abramov, 1954); in winter they eagerly visit ice crusts, including those in marshes, and lick them (Cherkasov, 1884; Fetisov, 1953).

Home range. Throughout the year, except for autumn and spring migrations, herds and solitary roe deer are confined more or less to definite home ranges, but when their populations increase to a considerable size their home ranges overlap one another. Observations have been made in Slovakia of the active defense of territory by some males outside the period of rut against other males (Dyk, 1956). Home range size is greater in transitional seasons (spring and end of summer to early winter); in autumn even resident roe deer wander 10 to 20 km a single day within a home range of up to 10 km in diameter (Sabaneev, 1875; Ushkov, 1947). With snowfalls and an increase in snow level, the radius of daily travel decreases, becoming least in the latter half of winter and in the period of snow crusts. At this time of year some herds of roe deer live for a few days or even a week in an area of 0.3 to 2.0 hectares (western Caucasus, Belovezh Forest, and Trans-Urals).[178] In summer, except for the period of fawning and the first one or two weeks after it, roe deer wander much more widely than in winter. When water supply is inadequate, they walk several kilometers in search of a water source (Naurzum pine forest).

---

[176] Instances are known of captured roe deer with their stomachs filled predominantly with pasque flowers, which are deleterious to cattle (Fetisov, 1953).

[177] In the Crimea acorn shells sometimes form up to 30% of the weight of the stomach contents of roe deer in winter (P.A. Yanushko).

Daily activity and behavior. In summer roe deer graze in the morning, evening, and at night, but at intervals (Averin, 1949; Fetisov, 1953). When the day is hot, they rest and ruminate, often lying in dense grass, among ferns, bushes, or wind-felled trees, eat grass or leaves only in the proximity of the bed and usually in small amounts. In cloudy and cold weather they often feed during the daylight hours. They seek refuge from blood-sucking insects in rocky open forests, on windblown banks of lakes, and in dense vegetation.

In winter roe deer graze at any time of day but if frequently threatened by hunters lie low during the day, emerging stealthily when necessary into very dense sections of forests, glens, etc., and coming out at night to feed in swampy river valleys (Altai), etc. During blizzards they seclude themselves in forest thickets.

Roe deer can jump to a height of 2.0 to 2.5 m. In the warm period they sometimes bathe and swim well; during migration they freely swim through such rivers as the Angara, Yenisey, Ussuri, and Amur. The weight distribution on the hoof is high, 300 to 360 g per cm^2, as a result of which roe deer get stuck in deep snow. The critical height of snow cover for European, Caucasian, and Middle Asiatic roe deer is 30 to 40 cm and for Siberian roe deer 40 to 50 cm. On experiencing difficulties in movement on snow roe deer often use their own old tracks or tracks made by other ungulates to reach main thoroughfares.

Smell and hearing are well developed in roe deer; in detecting danger they are guided to a lesser extent by vision than by olfaction and audition.

In summer adult roe deer are solitary (females move with their young) and only rarely are two or three (usually males) encountered together (up to seven in exceptional cases). At the end of rut, in September–October, mixed groups (males, females, and young) sometimes form, consisting of 20 to 30 animals or more.[179] At the

---

[178] According to Fetisov (1953) and Dul'keit (1956) solitary animals and herds of roe deer live within a home range of 1.0 to 6.0 sq km throughout winter.

[179] In the Urals in the mid-1800's herds of roe deer comprised as many as 50 to 100 or even 500 animals in the period of autumn migration (Sabaneev, 1875); in the snowy winter of 1940 to 1941 groups of roe deer numbering 50 to 120 animals were sighted in Il'men preserve (Ushkov, 1954).

conclusion of autumn migrations these groups usually break up
207 into smaller ones consisting of two to four each or slightly more. In spring, in April, with the approach of the fawning season, even these groups usually split up. Thus the gregarious tendency of roe deer is maximum in autumn, followed by winter; to some extent, it is directly proportional to the total population of roe deer and the degree of snowiness of a given winter. The herd composition does not remain constant even for one month, let alone two; groups of over 10 to 15 animals split up rather readily.

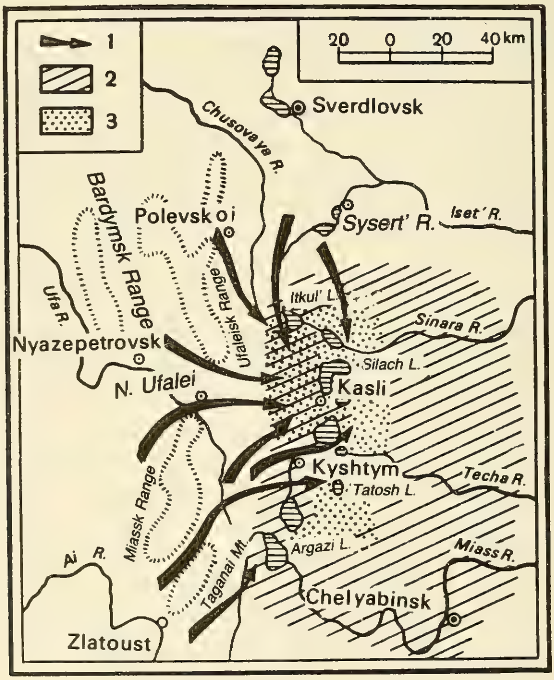
Seasonal migrations and transgressions. Seasonal migrations are characteristic of roe deer in many parts of the range. The course of these migrations is determined largely by the snow cover regime and the food regime. Migrations occur in autumn into less snowy regions and in spring into summer pastures and are particularly characteristic of forest-steppe zones (southern Trans-Urals, Kulundinsk, Minusinsk, and Achinsk steppes, Trans-Baikal, etc.), the Amur basin (in the past even in the Ussuri), and some northern parts of the range, but only in those areas where roe deer are fairly numerous (basins of the Chulym and Yenisey Rivers, Pri-Baikal, and Vitim plateau). Extensive migrations are common in many montane regions with relatively high (over 40 to 50 cm) snow cover (the Caucasus, Altai, Sayans, and others). The spatial magnitude of the seasonal migrations of roe deer goes up (at least it did in the recent past) in the Amur basin to 200 to 300 km [*sic*], and in the Urals, Abakansk range, Kuznetsk Alatau, and western Trans-Baikal to 100 km or more. A few centuries ago seasonal migrations of roe deer into places which combined different topographic sections and zones were characterized by an even broader spatial magnitude and were observed in a much larger number of regions in the country, for example in the
208 Ukraine (Nasimovich, 1955). In forests of the European part of the USSR and at places in other parts of the range seasonal migrations of roe deer are presently poor and involve displacement from one type of habitat to another within a few kilometers.

Forest sections with abundant young deciduous trees and undergrowth, low-snow steppes (especially in Trans-Baikal and in Minusinsk depression),[180] lower less snowy mountain altitudes, and generally places in which winter conditions are not very severe serve as places of winter congregation of roe deer. The range of vertical migrations usually does not exceed 500 to 800 m. In some montane regions roe deer spend part of the winter even at a higher level than in summer by congregating along windblown areas (Trans-Ili Alatau and Kungei Alatau).

---

[180] Roe deer are confined only in the warm period of the year to steppe zones where the snow regime is more severe (Kulundinsk steppe), and move away into forest sections in winter.

Migrations of roe deer to wintering sites occur in different parts of the range from mid-September to January and continue for three weeks to two months or more. Autumn–winter migrations usually commence with the first snowfall, particularly if the snow cover forms immediately, and rarely with the onset of sharp cooling. In mid-September, migrations commence in the Kuzetsk Alatau mountains, in eastern Sayan, Vitim plateau, and Zeya basin; the last migrations take place in December in the mountains of the Trans-Ili Alatau. In most of the remaining regions in the Soviet Union migrations of roe deer usually commence in October and end in November, usually earlier than in the case of elk and Manchurian wapiti. Dur-


1
2
3
20 0 20 40 km
Sverdlovsk
Chusovaya R.
Bardymsk Range
Polevskoi
Sysert' R.
Iset' R.
Ufa R.
Ufaleisk Range
Itkul' L.
Sinara R.
Nyazepetrovsk
Silach L.
N. Ufalei
Kasli
Kyshtym
Techa R.
Tatosh L.
Miassk Range
Argazi L.
Miass R.
Ai R.
Taganai Mt.
Chelyabinsk
Zlatoust

207 Fig. 64. Regions of winter congregation of roe deer from the 1860's to the 1870's in the Trans-Urals in the Iset River basin and its tributaries (scale in km).

1—course of travel of roe deer to wintering sites; 2—region under influence of snow; 3—places of winter congregation of roe deer. Scheme based on data of Sabaneev, 1872 (from Nasimovich, 1955).

ing migrations roe deer move in groups, sometimes in tens; herds of 100 to 500 animals have been recorded in the past. Spring migrations occur in April–May within a much reduced period (Nasimovich, 1955). A few decades earlier an immense number of roe deer moved away in autumn and early winter from the left bank of the Amur into Manchuria; in most places roe deer cross the Amur only on ice. The points of crossing of migrating roe deer over rivers (on ice and by swimming) are usually fixed.

The distance covered and vertical range of seasonal migrations also depend on the snowiness of a given winter. For example, in Crimean preserve, judging from the relative frequency of roe and red deer, only 5 to 7% of the summer population of roe deer in less snowy winters move out of the sanctuary down the slopes, while over 60% do so in highly snowy winters (P.A. Yanushko). At some places, in the latter half of winter, after a perceptible rise in the height of snow cover, fresh movements of roe deer are observed, which are sometimes more significant than those at the commencement of winter (the Caucasus, southern Trans-Urals, left bank of the Amur, etc.).

In Middle Asia and sometimes in the Caucasus individual roe deer emerge in summer into high mountain meadows, and in southern Siberia balds. Instances are known of migrations of roe deer during summer droughts; for example, in the summer of 1951 many roe deer from Belovezh Forest preserve, hit by drought, migrated into the territory of adjacent Poland (S.S. Donaurov).

Reproduction. In most regions mass rut in roe deer occurs in the latter half of summer, sometimes covering early autumn (up to mid-September), but usually lasting no more than a month in a given year. The earliest period of commencement of rut is mid-July, but even earlier in certain years; this is especially true of western parts of the geographic range (western Europe,[181] Baltics, western Ukraine, and Belorussia) and evidently also of Primor'e territory. In Latvia rut in roe deer sometimes commences from the end of June; in rare instances it has even begun from the middle of that month (Kalnin'sh, 1950). Mass rut in roe deer commences from the end of July to early August in the Crimea, Caucasus, southern Urals, in Trans-Urals and most regions of Middle Asia, i.e., in regions with extremely diverse climatic conditions. The very last period for the commencement of mass rut is August 5 to 15 and is typical of western
209 and eastern Siberia (plains of western Siberia, the Altai, Sayans, Pri-Baikal, Trans-Baikal, Hentei in Mongolia, Yakutia, and else-

---

[181] Excluding montane regions where rut usually commences two or three weeks later.

where), i.e., regions with a definite continental climate. There is almost no doubt that this relates to the duration of winter and later to a cold spring, which is unfavorable to early fawning. Thus, from west to east (excluding Primor'e) the period of commencement of mass rut is, in general, steadily delayed.

Rut usually terminates in the latter half of August and early September in western sections of the range (including Baltics, the Ukraine, and Belorussia), Crimea, Primor'e, and at places in the Caucasus and Middle Asia. In the Urals, western and eastern Siberia, and at places in the Caucasus (Armenia) and in Middle Asia (Kungei Alatau) the period of rut extends up to mid-September, and in some years even up to the last ten days of that month or even early October (Pri-Baikal, Trans-Baikal, and Yakutia). In Crimean preserve mating was observed once in December (Dal', 1930); such instances in October–November are known for many regions.[182]

Available data are inadequate to draw any distinct geographic patterns of the extent of regularity in the period of rut of roe deer in different regions. The commencement of rut, its intensity, and overall duration in different years depends on a combination of several factors: the nature of the preceding winter and spring (in arid regions also the type of summer in the preceding year), weather conditions in the summer of a given year, and other conditions which determine the general well-being of the animals. At places where these conditions are most constant year after year the commencement and duration of rut are also most constant.

Roe deer become sexually mature in their second year, but many breed only a year later; this is particularly true of males which otherwise cannot withstand successfully the competition from older and more powerful rivals. Young animals breed later than older ones. Among adult females as many as 10 to 20% may remain barren.

During the period of rut males are extremely high-strung, cast off their usual caution (instances are known of their attacking men[183]), and emit a chuckling sound. Combats between males are frequent and sometimes end with injury to, or even the death of, one or both competitors. In the period of rut a male lives for a few days with a single female, mating with her several times. In rare instances two or even three males may cover a single female during the same period (Sabaneev, 1875; and others) or a single male cover two or three adult females. The male chases away the offspring, which rejoin the female only after rut terminates. The female remains in a state of estrus for four or five days (Kalnin'sh, 1950). As soon as a female becomes unresponsive the male runs after a second and sometimes even a third. Roe deer therefore exhibit facultative polygamy.

---

[182] References by Sabaneev (1875) to instances of mating in March between young roe deer in the Urals beg credulity.

[183] Such instances also occur at other times of the year.

The pursuit of a female by a male usually occurs in a clearing or the edge of a forest. The female endeavoring to escape her unwanted suitor often circles round a tree, boulder, stump, etc., as a result of which the turf and grass there are trampled down. Instances are known of rutting males inflicting mortal injuries on females and young deer (Averin, 1949; and others). Males in rut eat little and lose considerable weight.

The fertilized egg travels along the oviduct for a few days, undergoes cleavage, and enters the uterus. There it remains in a state of relative inactivity, cleavage progresses slowly, and blastocyst formation is delayed roughly up to December. Only from the end of December or in mid-January is the fetus perceptible to the naked eye. The commencement of active growth of the fetus is sometimes
210 accompanied by excitability, similar to the behavior of martens during pseudoestrus. Among females mating in November–December delayed implantation is usually absent and embryonic growth commences immediately; fawning usually occurs at the same time as in females which mated in the latter half of summer (Lavrov, 1929; Kalnin'sh, 1950; Kirshenblat, 1951; and others[184]). Thus gestation can vary from 6 to 10 months; in most cases it extends over slightly more than 9 months (about 40 weeks).

In the western part of the range, as in the Crimea and Caucasus, mass fawning occurs in May. In some years some females fawn at the end of April,[185] while others do so only in the first half of June. In the Urals, western and eastern Siberia, and also in most Middle Asian regions mass fawning occurs two or three weeks later, commencing in the latter half of May to early June and ending around June 15 to 20; compared with the western parts of the range (Crimea and the Caucasus), fawning here occurs more uniformly. The young appear in Primor'e territory roughly around the same period as in Siberia.

In some instances roe deer give birth much earlier or later than the period indicated above. In Crimean preserve instances of fawning have been registered on April 7 (1950) or even on March 1 (1948)

---

[184] The main patterns of egg development in roe deer were first studied by Bischoff (1854).

[185] In the western parts of the Ukraine some females give birth to young even by early April (Tatarinov, 1956).

(P.A. Yanushko), in the Irkutsk region in the first ten days of July (Fetisov, 1953), and in Il'men preserve on July 14, 1938[186] (Averin, 1949).

In rare instances up to five (Sablina, 1955) or even six (Cherkasov, 1884) embryos have been detected. Some were evidently resorbed or the young stillborn since instances of even four fawns with a single female are exceptionally rare (observed in the Crimea, Il'men preserve, and elsewhere). Roe deer in most regions of western and eastern Siberia often bear two fawns, rarely one, and even more rarely three. Instances of triplets there are notably more frequent than in other parts of the range where climatic conditions are less severe. One or two fawns are usual in the Urals,[187] Middle Asia,[188] the Caucasus, Crimea, and at some places in the western parts of the range where the fertility of roe deer is usually somewhat less. Thus, of the 92 female roe deer with fawns counted in Crimean preserve in the summers of 1947 to 1950, 60% had one fawn each and 40% two each (deer with three or four fawns were not seen in those years) (P.A. Yanushko). In Belovezh Forest 169 roe deer were marked with young in the summers of 1945 to 1949; of these, 57.5% had one fawn each, 41.6% two each, and 0.9% (one deer) three (Sablina, 1955). In Il'men preserve 36 roe deer were found with fawns from May to July, 1938 and 1939; 50.9% had one fawn each, 43.3% two each, 3.9% (two deer) three, and 1.9% (one deer) four (Averin, 1949). Thus the average number of fawns per mother deer in these parts of the range for the summer period was 1.3 to 1.4.

Growth, development, and molt. Newborns remain stationary for a week, concealed in the grass. In the case of two or three fawns they do not remain together but stay at some distance from each other. At the age of six to eight days they begin to move away from the mother. At the end of two weeks fawns are not inferior to their mother in their ability to run.

Lactation continues for two or three months and ceases just before the onset of estrus. The latest date for lactating females is
211 October 20 (Fetisov, 1953). The young commence grazing on grass at the age of one month. In the period of estrus fawns remain aloof and join their mother later, after which they move together until the following spring.

---

[186] The first fawns in that year were observed on May 10. Thus the overall duration of fawning exceeded two months.

[187] According to Sabaneev (1875) three embryos used to be common in the Urals, while instances of females bearing four were not so rare.

[188] Instances of triplets have been recorded in Narynkol' region of Alma-Ata district (Zhirnov, 1958).

Two fully formed fetuses (males) covered with hair were removed from females caught in Belovezh Forest on July 7; they weighed 950 and 1,230 g. In the first half of July fawns reach a weight of 5.5 kg or slightly more (Sablina, 1955). Newborn roe deer are exceptionally light in coloration and their spots not as sharply defined as at the age of two or three months when a coarser beard [guard hairs] forms and the background color becomes darker. The spotted juvenile coat molts into the unspotted adult coat during August or at places even from the end of July.

Roe deer are born with all their milk incisors and premolars. Loss and replacement of milk incisors with permanent teeth take place at the age of 5 to 12 months; milk premolars are replaced with permanent ones at the age of 13 or 14 months. Molars begin to appear at the age of three months. In winter the rate of dental growth slows down but intensifies again from May; teeth are fully formed by the age of 15 months (Sokolov, 1956).

Antlers become visible in young males from the autumn of the first year in the form of small "pipes"; growth ceases only by April of the following year. Usually (but not always) they have a single beam without tines. The first antlers are shed in December and new ones become evident in January, which keep growing until spring; by then, the total number of tines on each antler is two or three. Often, even by the third year, antlers attain full development with, usually, three tines each. According to observations made in the Baltic region roe deer antlers grow best in areas where the soil is rich in phosphates and calcium salts (Kalnin'sh, 1950). Among adult males antlers grow from the end of March to early May. Shedding of velvet ceases by May–June, ossification is completed a little later, and antlers are shed in November (at places from the end of October and just before December[189]). In young males, compared with older ones, antlers grow roughly two to four weeks later and sometimes only in June in the Crimea (Dal', 1930). Antlerless males and females with antlers are not uncommon. Deformed antlers are also not infrequent.

Roe deer molt once a year, in spring. In January–February the hair is perceptibly worn out and shedding commences in March–April, initially from the sides of the trunk below the shoulder blades, later from the legs, head, and neck, and last of all from the rear of the back. Depending on the condition of spring, molt usually peaks the latter half of April to early May and ends in June and in rare cases in early July. In the montane regions of the Caucasus molt commences a month or so later than in the lowlands (Radde, 1889). The young generally molt slightly later than adults.

---

[189] Instances are known when roe deer shed their antlers even in September (Crimea; P.A. Yanushko) and, contrarily, when antlers were still present even in early January (Irkutsk region; Fetisov, 1953).

The summer hair coat consists of uniform guard hair which is sparser than in winter. Growth commences from August when underfur is also seen. In October the rust-colored summer coloration alters to a dark brownish-gray. After this the guard hair develops only insignificantly, lengthening up to December when it is longest and already duller than in autumn. When autumn is cold the winter coat develops earlier.

At the age of 10 years teeth start falling out and females become barren. The maximum age of females is usually 11 or 12 and of males about 16 years (Kalnin'sh, 1950).

Enemies, diseases, parasites, mortality, competitors, and population dynamics. Over much of the range the wolf is one of the main
212 enemies of roe deer. This predator subsists at some places mainly on roe deer, as a result of which its seasonal distribution and movements are often determined by the corresponding phenomenon in the life of roe deer (Podarevskii, 1936; and others). In Belovezh Forest, which is rich in some species of ungulates, remains of roe deer constituted 18.4% of wolf food (in over 1,100 samples of feces and stomach contents collected from 1946 to 1950). Wolves wreak maximum damage in winter. For example, in the winter of 1946 to 1947 when the snow height in Belovezh Forest was 55 cm, roe deer remains were seen in 28.2% of the food of wolves (Gavrin and Donaurov, 1954). In Il'men preserve roe deer are the main species of ungulates and their remains were found in 95.9% of all the data on food (395 samples) of wolves (in the summer 84.7%, winter 99.2%, and spring 100%). In this preserve 10 to 12% of the roe deer population are killed annually by wolves (Averin, 1949). Wolves cause exceptionally great damage to roe deer in Bashkir (Kirikov, 1952) and Irkutsk districts (Fetisov, 1953), Yakutia (Belyk, 1948), Primor'e territory (Abramov, 1954), and elsewhere.

Compared to wolf, all other predators are less important except, perhaps, for lynx (yellow-throated marten in Primor'e territory and red fox for European roe deer). In Altai preserve roe deer remains constituted 58.9% of the number of all quarries of lynx (56 observations on the tracks of lynx; Dul'keit, 1953). Thus roe deer represent the main food source of lynx in the Altai. Similar findings with respect to lynx and roe deer have been recorded in the central Urals (Sabaneev, 1875) and the Caucasus (Dinnik, 1910; and others). However, roe deer remains were found only in 3.6% of the data (136 samples) on feces of lynx from Caucasian preserve (Kotov, 1958). In the feces of lynx from Belovezh Forest the remains of roe deer were found in 20% of the total available data (Yurgenson, 1955). In some regions (Urals and Altai) lynx follow close behind roe deer during their migration to wintering sites.

Red fox often attack young roe deer, especially in the first few weeks after birth. However, in Crimea even adult roes, mainly emaciated and sick females, are also attacked frequently. From 1937 to 1940, when the fox population in Crimean preserve was very high, about 200 roe deer were killed annually by them. In those years over 50% of all established cases of death of roe deer were due to attacks by fox (Rukhlyadev, 1948). Epizootic diseases decimated the fox population of Crimea in 1946 and 1947. Yet in 1948 and 1949 fox were responsible for 36.8% roe deer mortality (P.A. Yanushko). Very large numbers of roe deer have been killed by fox in the Crimea in snowy winters (Dal', 1930; and others). In Germany the fox is regarded as the main enemy of roe deer; the maximum number of adult animals are killed by fox in winter when the snow cover is thick and crusts have formed (Raesfeld, 1956). In the Urals, the Caucasus, and especially in Siberia, where the large form of roe deer lives, fox almost exclusively attack the animals in their first year.

Many other predators, including some birds, can be considered enemies of roe deer but their role in population regulation is not significant. Such predators are bear (more dangerous for young deer), wolverine, tiger, leopard, red wolf, jungle cat [*F. chaus*], wild cat [*F. silvestris*], marten, golden eagle, eagle-owl,[190] and others, which threaten the life of young and juvenile roe deer. Wandering wild dogs take quite a large toll of roe deer; for example, in April, 1941, at the end of a snowy winter in Bashkir preserve 17 deaths of roe deer caused by wandering dogs were recorded (Kirikov, 1952).

In severe and snowy winters, and also in winters with prolonged ice crusts, not only are a large number of roe deer killed by wolves and other predators, but many die due to emaciation, diseases,[191] etc. Instances of mass mortality of roe deer in such winters are known in
213 much of the range and have been described time and again in the Crimea, the Caucasus, the Urals, southern Siberia, etc. (Nasimovich, 1955). In Latvia, in the severe winter of 1939–40 about 20% of all roe deer died (Severtsov, 1941). After the snowy winters of 1945 to 1947 roe deer were totally decimated at some places in the central Urals

---

[190] Remains of roe deer fawns were found in nests (Fetisov, 1953).

[191] Especially inflammation of the lungs occurring after prolonged chases by predators and the subsequent intake of snow by the flushed animal (Ushkov, 1954).

and reappeared only after some years. In the steppe regions roe deer are threatened by glaze ice which facilitates wolf chases of ungulates. A large number of roe deer died in the winter of 1948–49 in central and southern Kazakhstan when ice crusted on the heavy snow cover (Sludskii, 1953). In the mountains of western Caucasus death of roe deer due to snow avalanches has been reported (Nasimovich, 1955).

Roe deer are exposed to several infectious diseases: foot-and-mouth disease, cattle plague, Siberian ulcers, necrobacillosis, erysipelas, salmonellosis, tuberculosis, pasteurellosis, pyroplasmosis, and others. Some were detected in Crimean preserve (Rukhlyadev, 1939 and 1948), in the Caucasus (foot-and-mouth disease; Dinnik, 1910), and Moscow Zoological Garden (Sludskii, 1954; Fromkhol'd, 1958). Instances are known of mass mortality of roe deer due to epizootic diseases, the reasons for which are yet to be explained: in 1910 and 1912 in Belorussia (Serzhanin, 1953), 1926 in Azerbaidzhan (Lavrov, 1929), 1930 in Dzhungarsk Alatau (Shnitnikov, 1936), etc.

Eighty species of helminths have been identified in European roe

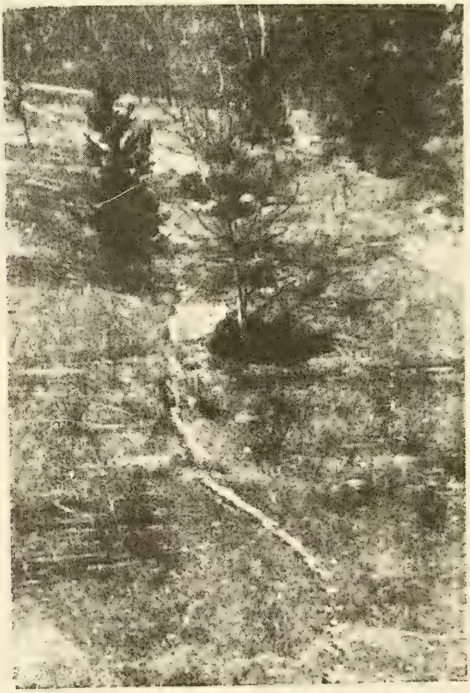


Fig. 65. Track of roe deer climbing a mountain. Middle course of Kan River. Irbeiskoe region of Krasnoyarsk territory. March, 1952. Photograph by K.T. Yurlov.

deer alone; of these, 68 have been recorded in the USSR (Belyaeva, 1958). In the Crimea moneziasis of the intestines and dictyocaulosis of the lungs are particularly dangerous, sometimes causing roe deer mortality (Rukhlyadev, 1948). Many roe deer are severely infected with different varieties of *Trichostrongylus*, which attack the respiratory tract and in zoological gardens often lead to animal mortality. Cases of coenurosis have also been recorded. Roe deer of Aksa-Dzhabaglinsk preserve were once severely infected with *Skrjabinema ovis* (Boev et al., 1957). In Crimean preserve 12 cases were confirmed of roe deer mortality due to theilerosis, a disease caused by blood parasites (Rukhlyadev, 1948).

Nasopharyngeal (*Cephenomyia stimulator* and *Pharyngomyia picta*) and dermal (*Hypoderma capreoli, H. diana,* and others) gadfly larvae parasitize roe deer. Larvae of *C. stimulator* sometimes penetrate the trachea and brain of roe deer. In Germany such events occurring in the period when the larvae of *C. stimulator* attain large size (April–May) may account for 55% of the annual mortality of this species (Grunin, 1957). Among other parasites of roe deer are the blood-sucking *Lipoptena cervi,* hair louse *Trichodectes tibalis,* and itch mite *Sarcoptes (Acarus) scabei.* Roe deer also suffer from horse-flies, mosquitoes, gnats, ticks, etc.

The most serious competitor of roe deer among the ungulates is the red deer. The adverse influence of the latter on the population of roe deer (destruction of winter food resources) has been observed in Belovezh Forest, Altai, and Crimean preserves, but as yet not adequately studied. Wild boar used to destroy large numbers of roe deer fawns in the Crimea (Dal', 1930).

A large number of young roe deer evidently die in the first few weeks or months after birth. In summer months the young constitute 26.9% of the total roe deer population in Crimean preserve; by the end of winter they comprise only 15.4% (P.A. Yanushko). In Belovezh Forest, depending on the severity of winter and the wolf population, 49 to 80% of roe deer young have perished by spring in various years (Sablina, 1955). Judging from long-term observations in Il'men, Crimean, and Belovezh Forest preserves, females predominate in roe deer populations and account for 54 to 68% of adult animals. At birth the sex ratio is nearly 1:1 or even slightly in favor of males. Thus the mortality of males is somewhat more than that of females and evidently the result of death during combat, emaciation during rut, and so on.

In Gatchina (Leningrad district), where 59 Siberian roe deer were released in 1896, the herd growth over a 12-year period averaged 26%. In some game farms of western Europe the herd growth index is much higher (Severtsov, 1940 and 1941).

Field characteristics. Roe deer are of relatively low stature (height at withers usually less than 90 cm versus 130 to 160 cm in red deer) and have a relatively short trunk and small, almost erect antlers with a limited number (up to three) of tines. These features make identification of roe deer among other members of the deer family quite easy. In summer the main coloration is rusty, much lighter on the lower parts, and the speculum around the tail poorly defined. In winter the general coloration is gray or grayish-brown, sometimes grayish-rusty, gradually darkening toward the rear and turning lighter downward, and the light-colored speculum around the tail is distinct. Young are spotted in the latter half of summer. Females are only slightly smaller than males; in winter, when males have no antlers, their differentiation from females at a distance is quite difficult. The neck in males is very short and thick and the hair hangs down under the abdomen (Kalnin'sh, 1950).

Roe deer hoofprints are small, blunt, and rounded in males and relatively long and narrow in females. When moving slowly the distance from the center of one print to that of another averages 45 cm in adult Crimean roe deer; they usually jump 1.5 to 2.0 m but when very frightened even up to 7.5 m (Dal', 1930).

In winter roe deer try out several places (up to six) before selecting a bed. A bed in snow is very small and not equal to the body size since the legs are tucked in. In regions with severe winters roe deer usually lie on the ground and leaves after scraping away the snow first; they often lie directly on dry snow, however. In winter males are readily distinguished from females by the position of the brown urine patch on the track.

In winter feces are in the form of longish pellets (10 to 14 mm ×6

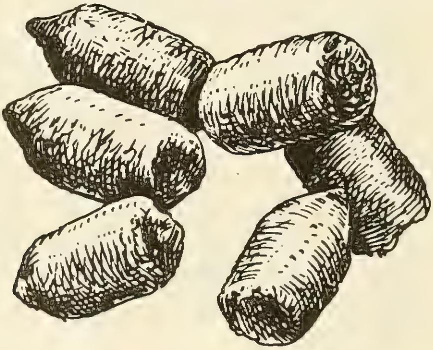


Fig. 66. Winter feces of roe deer (magnified 1.5 times). Primor'e territory (from Formozov, 1952).

to 9 mm) and in spring formless cakes; both types of feces are seen in summer. The pellets are much smaller (0.7 mm × 0.4 mm) for six-month-old deer. Identification of sex from the form and size of feces is unreliable.

215 In the period of rut roe deer stamp out characteristic circles around trees, beat the turf, batter branches of shrubs with their antlers, etc. (see above). Unlike red deer and elk, roe deer never touch bark. Like other ungulates, they often make trails, especially near salt licks, etc.

Roe deer emit a prolonged squeak and a short, interrupted, very loud, and hoarse bellow ("gau, gau"); females bellow very rarely and their voice is less coarse. Roe deer call most often when frightened. The young emit a high and prolonged squeak.

In winter roe deer seldom, if ever, bark. (A.N.)

Economic Importance

Throughout most of the nineteenth century, and at some places in the first two decades of the twentieth, roe deer were caught in the Soviet Union in very large numbers. Hunting roe deer was particularly practiced in southern Siberia, the Far East, and the Urals, acquiring commercial proportions. The largest number of roe deer were caught in winters of heavy snow. For example, in the excessively snowy winter of 1877–78 about 150,000 roe deer were caught in the Amur region (Turkin and Satunin, 1902). Mass shoots were carried out in autumn and early winter at places of migration of roe deer on ice and while swimming across the Amur, Ussuri, and to a lesser extent also across the Yenisey, Abakan, Bir, Irtysh, and other rivers. In the Amur hunters following "moving goats" [roe] for 200 to 300 km; in successful years a hunter bagged 50 to 100 deer (Nasimovich, 1955).

Various methods of mass capture of animals were practiced in different parts of the range: nooses and traps set in passages of specially erected fences, chasing in the period of migration, through deep snow, on ice, etc. Roe deer were caught not only in the cold season of the year, but also in summer—by voice imitation (luring females by imitating the voice of the young), at salt licks, in trails etc. The meat of roe deer represented an important food source in many towns of Siberia.[192]

Thoughtless and often savage hunting adversely affected the reserves of the species and the population of roe deer in most regions was depleted. For this reason after the October Revolution hunting was controlled in the Soviet Union; roe deer shoots were greatly restricted and at places totally prohibited (the Ukraine, Belorussia, and several regions of the Russian Soviet Federal Socialist Republic). In recent years maximum numbers of roe deer have been caught in southern Siberia[193] and Primor'e territory, reaching 40,000 to 50,000 animals per year, followed by Kazakhstan and Kirgizia (up to 5,000 to 10,000), the Urals, etc. In the Caucasus, Crimea, and Baltic region hunting is purely a sport, often limited only to males and that too on a very small scale, and at places not permitted every year. In the Asiatic part of the USSR the reserves of roe deer in general are quite considerable (see above) and hence a catch of 50,000 to 60,000 animals per annum is permissible. The most rational periods for hunting are October and November and from November onwards in the southern parts of the country.

---

[192] In the winter of 1887 to 1888 the carcass of a roe deer in the Blagoveshchensk market cost 1.60 to 1.70 rubles.

At present the most prevalent methods of hunting are: shooting from ambush, catching by use of pens, waiting at places of regular visitations and feeding grounds, chasing on sledges (in Siberia), etc. In spite of legislation prohibiting it, at places, for example the Altai, roe deer are increasingly caught in summer with mechanical traps or chased in winter (the Urals) on heavy snow and ice crust. Dogs are usually employed only for locating wounded animals. In the past hunting with hounds was often practiced in the Caucasus, the Urals, and elsewhere.

The net weight of meat from a southern Russian roe deer is usually not more than 14 kg and from a Caucasian an average of 15 kg, while Siberian and Middle Asiatic animals yield slightly over 20 kg (very rarely up to 30 kg), representing roughly 60% of live weight. Depending on size and fattening a roe deer can provide 1.5 to 2.5 kg fat. The meat of roe deer is less valued than that of other species of wild ungulates.

216 Roe deer hide is utilized for articles of apparel and chamois. Late September and October hide is considered the best and called "Barlow hide"; by December the hair has become less stable and the hide poor in quality. Hides are mainly used in fur coats (with the hair outside), caps, and more rarely other articles such as flying boots, mittens, sleeping bags, and cloaks. In the past hides were also converted into collars, jackets, breeches, belts, and saddle cloths; summer hides were used in small rugs, and so on. Fur coats are

---

[193] In 1924 about 47,000 roe deer were caught in Tuva Autonomous District alone (Yanushevich, 1952).

warm but shortlived since the hair falls out rapidly; properly cared for a coat may last three to five years. Antlers with the frontal bone serve as wall decorations (in the nineteenth and early twentieth century they were exported to Germany) and are also converted into small articles.

In cultivated areas roe deer inflict damage only when they occur in large numbers. Then they trample and browse tender saplings, damage winter crops (rye and others), and spring oats. In summer they damage cereal crops (in which they make beds), clover fields, and vegetable patches (trampling and eating potato tops); in winter they stamp hay left over in fields. In Belovezh Forest roe deer sometimes threaten self-sown pine (browse them in winter), oak, beech, and maple, but the damage by and large is insignificant (Sablina, 1955). In Il'men preserve aspen seedlings are most intensely damaged (100%), followed by pine and birch (40 to 50%). When 10- to 15-year-old pine and birch trees grow beyond the reach of roe deer they usually recover. Hence the damage to forest trees caused by roe deer is also insignificant (Averin, 1949). In Estonia roe deer damage most intensely aspen forests (heartrot extends from the point of damage on the trunk). In Latvia two- to three-year-old pines suffer and at places where roe deer are numerous even eight-year-old pines are not spared (Kalnin'sh, 1950). Judging from the experience gained in Czechoslovakia, the negligible damage caused by roe deer is more than compensated by the value of this species as a game animal.

Roe deer have been released time and again into private farms for purposes of raising them as game animals. In 1891 eleven Siberian roe deer were imported into Belovezh Forest[194] where they acclimatized and reproduced (Kartsev, 1903). The 59 animals released in Gatchina game farm (now in Leningrad district) in 1896 had multiplied to 1,068 animals by 1909 (Severtsov, 1940), but later became extinct there. Right up to World War I, 15 to 20 European roe deer were held at Ramon' (Voronezh district) in a pen (free roe deer there had disappeared). Later they were brought into Usmansk Forest where a few were conserved; they are now slightly greater in numbers (Nikul'tsev and Predtechenskii, 1957).

Commencing with 1925 small batches of roe deer from the Crimea and other places have been released in the Ukraine (Diken'ka, Pechenegi, and other regions); almost everywhere these roe deer were later killed by wolves, poachers, etc. Ten roe deer were brought from Kirgizia to Mordov preserve in 1940. After 1943 they were no longer sighted there [Letopis' prirody Mordovskogo zapovednika (History of Mordov Preserve)]. In 1932 and 1939 a total of 12 roe deer were brought into Zavidov game farm (north of Moscow) from the southern Urals. By 1941 they numbered 50 to 60 animals and by 1945, after the War, about 40 (Danilov, 1947). Roe deer are still seen in this farm. European and Siberian roe deer have been released time and again around Moscow on Losin Island. In 1941 there were about 80 animals—all killed during the War (Formozov, 1947). In 1950 and 1952 some were released in Sobin and Petushin areas of the Vladimir district. These animals survived, reproduced, and later spread into adjoining regions of the district (Sysoev, 1955). In 1954 ten Siberian roe deer were released in Pereslav game farm (Yaroslav district), and in 1957 forty (from Primor'e territory) in Dubna (Moscow district). Roe deer in recent years have been released in other regions of the Soviet Union also.

---

[194] Local roe deer were also present in the forest.

In nature roe deer are pugnacious, often attack man, and suffer from various diseases. (A.N.)

279

GENUS OF ELK*

Genus *Alces* Gray, 1821

1775. *Alce.* Frisch. *Natur-Syst. d. vierfüss. Thiere,* p. 3.

1821. *Alces.* Gray. *London. Med. Reports,* vol. 15, p. 307. *Cervus alces* Linnaeus.[195]

1841. *Alcelaphus.* Gloger. *Handbuch d. Naturgesch.,* p. 143. Substitute for *Alces.*

1902. *Paralces.* J. Allen. *Bull. Am. Mus. Nat. Hist.,* vol. 16, p. 160. Substitute for *Alces.* (V.H.)

Alces are telometacarpal deer of large size (the largest forms of the subfamily and family); heavy build with a relatively short trunk; high withers; large, massive, heavy, and highly elongated head; and long legs.

Hooves of middle toes narrow, long, and sharp; lateral hooves large and set quite low.[196]

Skull relatively large, highly elongated (width in region of zygomatic arch slightly over one-third its total length), with a well-developed facial part: distance from center of orbit to anterior tip of premaxillae roughly double the distance from center of orbit to rear

---

*Termed "moose" in North America, where the name "elk" is often applied to the wapiti (*Cervus elaphus*).

[195] In view of some confusion associated with the name *Alce* (often applied to giant deer), the International Nomenclature Committee has recommended the use of Gray's name.

[196] Functional, and facilitate movement on soft marshy soil and on snow.

level of occipital condyles (distance from anterior molar to end of premaxilla roughly 1.5 times upper tooth row). Nasal processes of premaxillae do not reach nasals. Latter very short, roughly one-third shorter than upper tooth row; nasal passage very large and markedly longer than upper tooth row. Preorbital depression on lacrimal bone well developed but small and set away from rim of orbit; ethmoid pit distinct. Rear of vomer low and does not divide posterior openings of choanae into two parts. Tympanic bullae very small, do not project beyond glenoid fossae, and covered with sharp bony projections; auditory meatus long. Bony pedicels of frontals set straight on sides (perpendicular to sagittal plane of skull) and fall in plane of frontal surface of skull (the only instance in the family). Lower jaw highly elongated. Height of symphysis nearly equal to length of tooth row.

Upper canines absent in males as well as females and their sockets closed (rudimentary canine a rare exception). Molars relatively large, massive, and broad with low crowns. Lateral walls of teeth incline inward, as a result of which masticatory surface is smaller than tooth base.[197] Incisors and lower canines relatively poorly specialized and differ little from each other in size and form. Dental formula:

$$i\,\frac{0}{3},\quad c\,\frac{0}{1},\quad pm\,\frac{3}{3},\quad m\,\frac{3}{3} = 32.$$

Only males sport antlers, which run straight out to the sides, quite horizontally, slightly turning upward near the end, and generally set sideways. Antlers either wholly (except for small section of beam at base) webbed with small tines set forward, sideways, and 218 backward, or, along with palmate portion exhibit a special tine quite separated from it (sometimes wholly and in others not so); this special tine is set forward and usually bifurcate at the end, or palmate portion not developed at all and antlers branched like those of "deer"; antler beam circular in section. Antler surface, especially of beam, uneven and rough; color deep brown.[198]

---

[197] In form and relative size molars of elk have common features with those of giraffe, evidently due to their feeding on similar types of food (branches).

[198] The homology of parts of elk antlers is difficult. The anterior tine of the corresponding part of the palmate portion is taken as representing a fused brow and middle, or second and middle, or only middle tine of a typical deer antler. Usually the brow tine is assumed to be absent in elk. The palmate portion is formed by the flattened end of the beam or the rear tines fusing together but set forward or sideways (as a result of a twist in the beam) (i.e., the palmate portion is homologous to the rear tines of reindeer and fallow deer). Thus, the rearmost inner tine (set toward the neck) would form the beam end and the tine in front of it would be the rear one.

Ears very long and broad. Tail short. Muzzle, i.e., upper lip and nasal region, very large, broad, and viewed from the front, appears cut in straight line ("squarish"); overhangs lower lip and has a complex inner cartilaginous skeleton. Muzzle covered with hair except for tiny triangular or rhomboidal patch situated midway on front lower surface of upper lip.

Dewlap, usually more prominent in males present on throat.

Preorbital glands well developed but not very large. Hoof glands present only on hind limbs and resemble saccate invaginations with a small opening on the anterior surface. Tarsal and metatarsal glands small; latter set high (at the level of calcaneal joint) on the inside of legs.

Coloration uniformly dark (blackish-brown or almost black), legs considerably lighter than trunk, and speculum on rear of thighs absent. Hair on neck and withers elongated. Coloration of young uniform (without light spots). Female somewhat smaller than male. Teats four.

These are inhabitants of taiga, mountain taiga, and mixed forests, with a preference for lakes and marshy regions, in part forest-tundras and forest-steppes, and bottomland deciduous forests in steppes. Evidently, unlike most other members of the family, they are monogamous.

The range of the genus is associated with the forest of the northern hemisphere and is divided into two parts—American and Asian.

In North America the range (reconstructed) occupied much of the forest zone (apart from purely deciduous forests). Its northern boundary in the northwest covered the Yukon basin, ran to the Mackenzie estuary, and descended from there in an irregular line to the southwest corner of Hudson Bay, and in the east to the St. Lawrence Gulf. Farther away the range encompassed all of Nova Scotia and New England (elk have been acclimatized in Newfoundland) and formed a prominent extension southward along the northern parts of the Allegheny mountains. More to the west the southern boundary ran through the region of Lake Superior (between upper [Lake] Michigan and Huron), and encompassed the northern parts of Wisconsin, Nebraska, and North Dakota; passing north of [eastern] Montana and southern Saskatchewan, it descended in the form of a promintory along the mountains up to the Yellowstone (around 45° N lat.). From there, gradually coming closer to the Pacific Ocean coast, the boundary departed northward into Alaska.

In Eurasia the range of elk (reconstructed) occupied the entire forest zone of Europe, in the west to the Rhine estuary and to the

Vosges; in the south up to the northern foothills of the Alps and to the Carpathians, part of the steppe zone (at least the Don basin and probably the Volga), the Caucasus and western Trans-Caucasus, all of the forest zone of Siberia including forest-tundra (at places even tundra) and forest-steppe, forest parts of Mongolia (Khangai and Pri-Hobsogol), forest regions of the Far East (except Kamchatka), the Ussuri region, and northeast China.[199] On the whole the range is extremely typical of circumboreal ranges of forest (mostly taiga) forms.

220 At several places the range of elk has shrunk and continues to diminish (America); simultaneously a perceptible enlargement of it has occurred in the USSR, mostly in the south and partly in the north.

The genus *Alces* occupies an extremely isolated position among present-day telometacarpal deer (Odocoileinae) and not one of the other genera of the subfamily reveals any close relationship to it. Some researchers have isolated this genus in a special tribe.

The origin of the genus cannot be explained with any degree of accuracy. A wholly typical form of it is seen in the Early Quaternary (Gunz) period. The genus *Alces* should evidently be derived from Pliocene *Eucladocerus* and its origin placed in the Upper Pliocene. The North American Quaternary *Cervalces* is close to *Alces*; the former in some respects can be considered intermediate between the two genera *Alces* and *Eucladocerus* (Flerov, 1950). *Eucladocerus* prospered in the Middle and Upper Pliocene and partly in the Early Quaternary period of Europe and Asia. Evidently elk, in spite of their affiliation to the predominantly American form of deer, should be considered as having originated in Europe.[200]

Some species of Pleistocene elk have been described but most of these descriptions are baseless. At least in the USSR only one independent Quaternary species occurred, the broad-fronted elk *Alces latifrons* Dawk., typical of the Lower Pleistocene. Its descendants survived in the Upper Quaternary period and by then bore resemblance to present-day species (Gromov, 1948). They were distributed somewhat more extensively than in the historic period and encoun-

---

[199] For datails, see description of range of elk given below.

[200] According to some paleontologists (Simpson, 1945) genus *Eucladocerus* is neither related to genus *Alces* nor even subfamily Cervinae; it has affinities with the giant deer (*Megaloceros*). Accordingly, only the Pleistocene North American *Cervalces* is associated with *Alces* as the most proximate and ancestral form. The origin of the genus *Alces* is thereby also shifted to American territory in which most other telometacarpal deer (Odocoileinae) exist and prosper. Giant peat deer, having huge antlers with palmate or webbed portions and externally similar in general to elk, according to a view commonly held, are not related to genus *Alces* either.

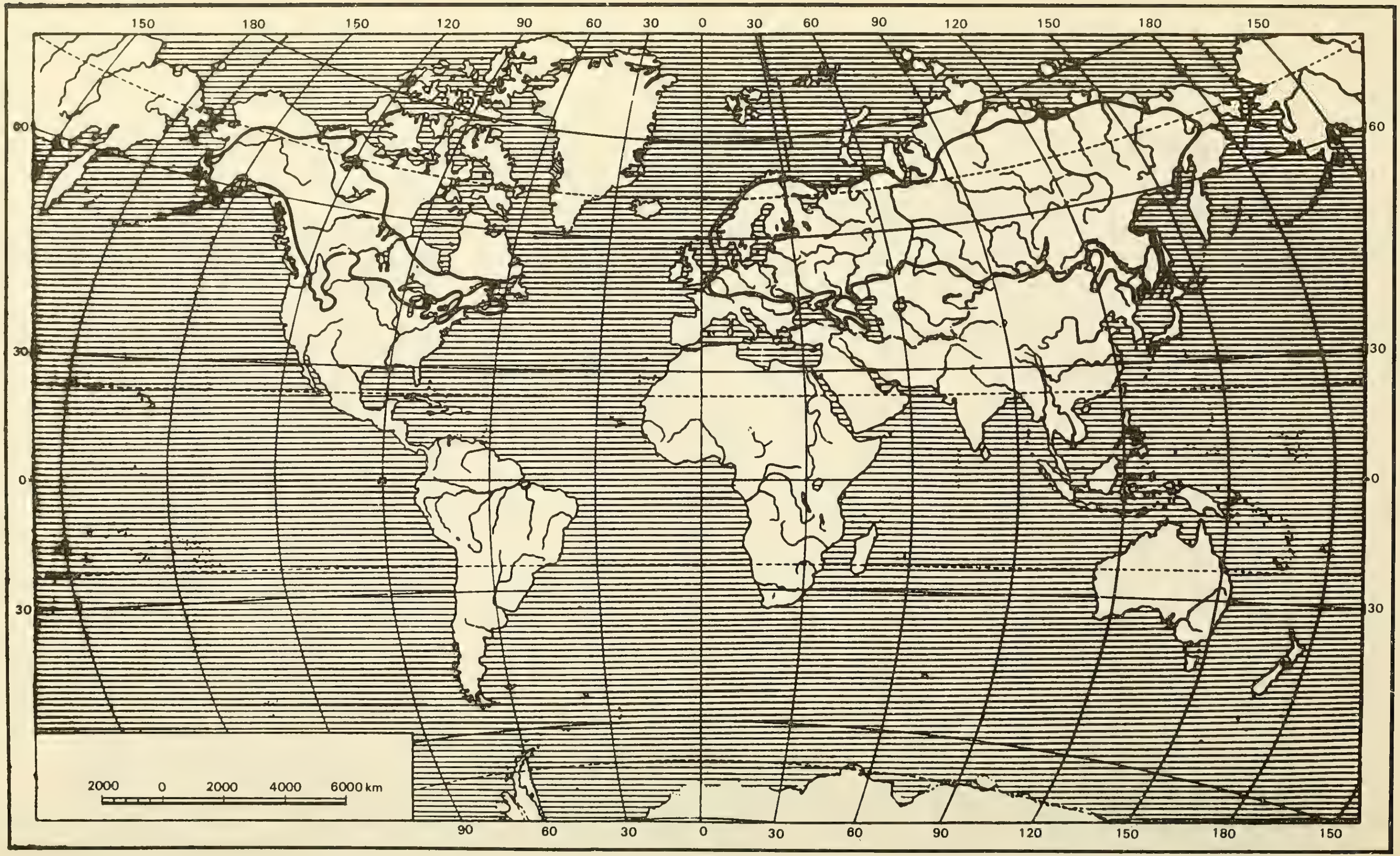

150
180
150
120
90
60
30
0
30
60
90
120
150
180
150
60
30
0
30
2000
0
2000
4000
6000 km

Fig. 67. Geographic range of elk genus (*Alces* Gray) and elk species *Alces alces* L. (scale in km). In the Old World boundaries given of present maximum dispersal and of the reconstructed range. Zone of summer visitations into tundra partly outlined. V.G. Heptner.

tered (often even in the Neolithic period) in the steppe regions of the Ukraine, lower Volga, Trans-Caucasus (Rion basin), on the Black Sea coast of the Caucasus, and in England and Ireland. In western and central Europe, however, elk did not penetrate south of the Pyrenees and were not found in the Balkan and Apennine Peninsulas.

Until recently the genus purportedly included four, three, or two species. Some contemporary American researchers still accept two species of elk, i.e., Eurasian and American. Yet it is absolutely clear that the genus consists of only one species, *Alces alces* Linn. (about 5% of the species of the subfamily).

These animals represent hunting and table animals and are sought for their meat and hide.

There is only one species of elk in the USSR, *Alces alces* Linnaeus, 1758 (0.3% of species of Russian fauna).

Elk are taiga and mountain taiga animals with a preference for swampy areas, partly occupying mixed forests, and more rarely forest-steppes, forest-tundra, and tundra.

Elk as hunting and table animals are very important at places (western Siberia) to the local populace. Hunting of elk is prohibited in many parts of the country or allowed only by special permission (license). (V.H.)

ELK, SOKHATYI[201]

6. *Alces alces* **Linnaeus, 1758**

222 1758. *Cervus alces.* Linnaeus. *Syst. Naturae,* 10th ed., vol. 1, p. 66. Sweden.

1785. *Cervus alce.* Boddaert. *Elench. animalium,* vol. 1, p. 135.

1822. *Cervus americanus.* Clinton. *Letters Nat. Hist. and Intern. Resources State New York,* p. 193. New York.

1827. *Cervus coronatus.* Lesson. *Man. de Mammal.,* p. 356.

1830. *Alces europaeus.* Burnett. *Quart. Journ. Sc. Lit. Art.,* 1829, 2, p. 353. Nomen nudum.

1837. *Alces machlis.* Ogilby. *Proc. Zool. Soc. London,* 1836, p. 135. Substitute for *alces* L.

1842. *Alces antiquorum. Rüppel. Mus. Senkenb.,* vol. 3, p. 183. Substitute for *alces* L.

---

[201] Male = los' [elk] bull; female = cow, losikha. Attempts (Flerov, 1935 and 1952) to introduce into the Russian language the popular American name "moose" for east Siberian elk should be vigorously opposed since there is no justification whatsoever for such usage.

1843. *Alces palmatus.* Gray. *List Mamm. Brit. Mus.,* p. 142.

1860. *Alces jubata.* Fitzinger. *Nat. Säugeth.,* vol. 4, p. 86. Substitute for *alces* L.

1867. *Alces cameloides.* Milne-Edwards. *Ann. Sc. Nat. Zool.,* vol. 7, p. 377. Manchuria.

1899. *Alces gigas.* Miller. *Proc. Zool. Soc., Washington,* vol. 13, p. 57. Kenai Peninsula, Alaska.

1902. *Alces bedfordiae.* Lydekker. *Proc. Zool. Soc., London,* 1902, vol. 1, p. 109. Eastern (?) Siberia.

1910. *Alces machlis typicus.* Ward. *Rec. Big. Game,* 6th ed., p. 99.

1910. *Alces pfizenmayeri.* Zukowsky. *Wild und Hund,* vol. 16, p. 807. Aldan River, Yakutia.

1911. *Alces machlis yakutskensis.* Millais. *The Field,* vol. 118, p. 113. Aldan River, Yakutia (name based on same material as in preceding reference).

1913. *Alces machlis uralensis.* Matschie. *Veröff. Institute Jagdkunde Neudamm,* vol. 2, p. 155. Southern Urals.

1913. *Alces machlis meridionalis.* Matschie. *Veröff. Institute Jagdkunde Neudamm,* vol. 2, p. 156. Samar province.

1915. *Alces machlis tymensis.* Zukowsky. *Arch. f. Naturgesch,* vol. 80A, no. 9, p. 42. Western Siberia, Tym River.

1915. *Alces machlis angusticephalus.* Zukowsky. *Archiv. f. Naturgesch,* vol. 80A, no. 9, p. 44. Yenisey province.

1928. *Alces alces bedfordi.* Bobrinskii. Opredelitel' okhotnich'ikh i promyslovykh zverei (Identification of Game and Table Animals). Ussuri region.[202]

1955. *Alces alces caucasicus.* Vereshchagin. *Zoologich. Zhurnal,* vol. 34, no. 2, p. 461. Urukh gorge, central part of northern slope of Great Caucasus. (V.H.)

Diagnosis

The genus *Alces* contains only one species.

---

[202] The author of this work attempted to identify precisely the typical habitat of the form described by Lydekker (1902) since it was shown in an extremely generalized manner. N.A. Bobrinskii mistakenly used the patronymic name given initially to the female form with a masculine ending. This error was repeated later by the author (1944) and by others. There is no basis for Bobrinskii giving this name to Ussuri elk, as assumed by Buturlin (1934), who recognized neither the slip nor error made by this author. In general this name and its given outline, initially accepted by Lydekker (1912), is no more than a synonym since Manchurian-Ussurian elk ought actually to be labeled *cameloides,* the name assigned to them in 1867 by Milne-Edwards.

Description

Large deer, the largest living species of the family. In general appearance very massive and powerful, somewhat heavy but well built. Build differs markedly from other deer, primarily in long legs, powerful and massive chest and shoulders, and large and heavy head. Neck and head usually held low and fairly horizontal.

Since the legs of elk are very long the trunk, though of normal length, appears relatively short and the withers high; the latter with
223 its long coat of hair forms a humplike structure.[203] Back straight, sacrum slightly lower than withers, croup relatively poor and sloping, tail very short, much less than one-half length of ear and not discernible in an active animal. Neck relatively short, thick, and massive. Head relatively very large, long (roughly equal to neck in length), narrow, and aquiline. Upper lip very large and massive, as though inflated, squarish when viewed from below, and prominently overhangs lower lip. Nostrils large and set low. Ears very large and broad, generally oval in form, but pointed at tips and highly mobile. Eyes relatively small. Small preorbital glands present. Dewlap fairly long with a triangular profile but sometimes sausage-shaped; its size maximum in animals three to four years old, becoming shorter and broader later. Dewlap length reaches 35 to 40 cm, usually 20 to 25 cm.

Hooves large, long, and narrow; strongly pointed forward. In females somewhat narrower and sharper than in males. Lateral hooves relatively large, set low, and when moving on soft soil rest on the ground and carry part of the body weight.

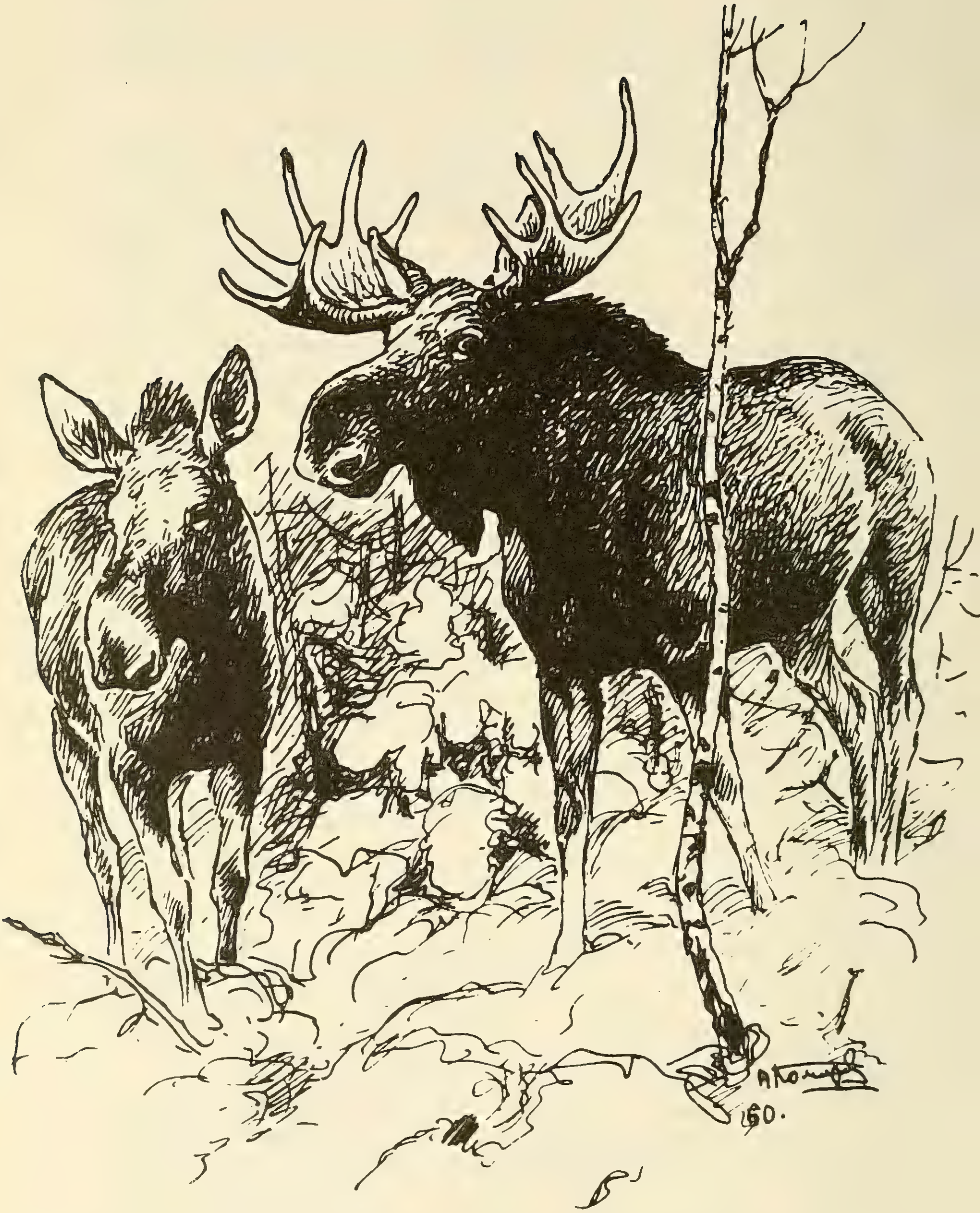
In general appearance cows are indistinguishable from bulls, but body build of former somewhat more slender and chest, shoulders, and withers less massive. In the first few months particularly sharp differences between trunk and limbs apparent in both sexes—a disproportionately small trunk on particularly long legs. Moreover their head is relatively small and the upper lip not swollen but nearly normal. In their first winter the body proportions of young elk stand out even more prominently compared to those of older animals; fairly typical proportions of adult animals are not attained earlier than in the second year.

Antlers of elk[204] are extremely variable in size and structure, more so than those of other Russian deer except, perhaps, reindeer. Age variability, regional variability, and sometimes extreme individual

---

[203] Elk, unlike other deer but like the giraffe, amble because of their long legs.

[204] See characteristics detailed under genus.



221 Fig. 68. Elk (*Alces alces* L.). Sketch by A.N. Komarov.

variability are apparent. Typical elk antlers consist of a short beam set off from the skull horizontally and perpendicular to the sagittal plane of the body. The plane of the flattened and fairly curved palmate portion is directed forward to a lesser extent, more sideways, but mainly backward. When the head is held in a horizontal position, the plane of the palmate portion is almost horizontal, rising slightly only in the rear. Tines are directed from the palmate portion forward, outward, and backward, but not inward (not toward the neck). They are also set slightly upward in continuation of the curved shape of the palmate portion. All the tines are more or less identical and form a frame around the periphery of the palmate portion uniformly, but more often the tine directed forward is larger than the rest and somewhat isolated from the palmate portion. Often, individual tines are quite independent even on the other parts of the palmate portion, but more often in the posterior or posterolateral parts; an appreciable indentation occurs in the palmate part.

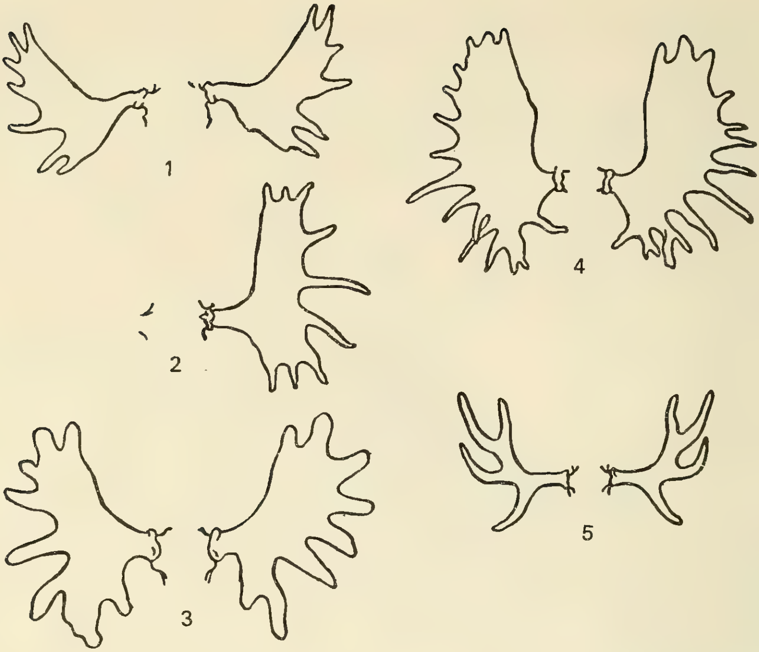
Antlers of this type may attain very large proportions. However, in most cases the flat zone of the palmate portion itself is small and the tines long. Usually, the larger the palmate part the shorter the tines and vice versa. Maximum-sized antlers have an extremely long and broad (up to 60 cm or more) palmate section with short tines, often with a prominent forward tine (on the palmate section) which bi- or trifurcates at its tip.

The second antler type is also palmate but a massive separate tine stands prominently forward and is usually bifurcate at the tip,
224 resembling somewhat two forward tines from the anterior part of the palmate section. Several intermediate varieties occur between this and the typical antler form. Both types are similar and differences only quantitative.

The third antler type—the "cervine" type antler, completely lacks a palmate section and the beam is fairly short and thick, symmetrically branching in a fairly horizontal plane. The tines are set forward, sideways, and backward, and upcurved.

Between the antler types described above, especially the first two, several transitional forms occur, each exhibiting wide variations. Antlers with a small palmate portion and long tines, usually with a massive bifurcate tine prominently set forward, are most common among Russian elk. The number of tines on particularly large antlers can reach 36 (on a pair of antlers) and probably even more. Some geographic similarities are seen in these types, especially in "cervine" type antlers (see "Geographic Variability").

Age-related changes in antlers are as follows. A two-year-old bull carries a small unbranched stump on which two tines (forks) form in



224 Fig. 69. Some types of antlers in elk (*A. alces*).

1—Well-developed palmate antlers of central Russian elk (*A. a. alces*); 2—large antler of elk from Bryansk region (maximum length 68 cm); 3—typical antlers of elk (*A. a. alces*) from western Siberia (Dem'yanka River); 4—unusually large antlers of western Siberian elk with long and broad palmate portion (Dem'yanka River); 5—typical antlers of Ussuri elk (*A. a. cameloides*). From Kaplanov (1948) and Flerov (1952), with some modifications; antler of Bryansk elk from A.V. Fedosov.

the third year. Later, the antler changes in no regular or fixed pattern except that generally the older the animal the larger and more massive its antlers, the larger the palmate portion, and the shorter the tines. In extreme old age deterioration and secondary simplification of antlers set in which, evidently, can be extensive.[205]

225 The hair of elk is similar to other deer—coarse, slightly wavy and thick, with air cavities (especially in winter pelage), and brittle. Winter hair on the trunk is about 10 cm or more in length and even slightly longer on the back. Hair is particularly long on the withers (about 16 to 20 cm) and on the upper part of the neck where it forms a characteristic mane. Long hair on the withers is largely responsible for the "hump" so characteristic of the general shape of elk. On

---

[205] The structure, development, variability, and other features of elk antlers have hardly been studied. This is particularly true of Russian elk.

the sides of the neck the hair is not so long, only slightly longer than that on the body sides.

The head is covered with short and slightly softer hair, which is particularly short but very resilient on the entire anterior part of the muzzle. Only at the center of the upper lip does a minute bare spot occur, which is oval, pyriform, or triangular in shape. It is so small that it stops far short of the nostrils. Sometimes, in addition to this bare spot, two other minute spots occur, one on each side of the former but closer to the nostrils. The lips of elk are covered with hair right up to the edge of the mouth.

On the legs, especially in their lower half, the hair is short and not wavy, slightly arcuate, resilient, and very strong, especially on the anterior side of the legs. This represents an adaptation in an animal which for most of the year moves through deep snow.[206]

The coloration of the trunk, the upper portions of the legs, the neck, and much of the head of an adult animal is a uniform, dense, brownish-black or nearly black. The tip of the muzzle is light gray, even whitish. The coloration of much of the limbs, roughly from the middle of the shin and foreshoulder, is light gray, sometimes nearly white with a silvery shade, and contrasts sharply with the overall color of the trunk.[207] Speculum absent.

There are no significant differences in the color of the summer and winter coats of elk. Only a single molt occurs, in spring, but it extends over most of the summer. Commencing in April molt is most intense in May and June and remains of the worn-out winter coat are still evident even in July. The complete short summer coat (August) is extremely dark, almost black, and shiny. Later, due to hair growth, the color gradually lightens by winter, becoming more brownish and dull. The wear and tear of dark hair tips in winter also contributes to the appearance of brownish shades. There are no sex-related color differences.

The coloration of newborn elk during their first few months (up to the first winter pelage) is a uniform dark or rusty-brown all over the body. The anterior portion of the muzzle and the legs are also of the same color. Sometimes a dark band occurs along neck and in the shoulder region on the back. Spotted coloration is never seen in the young.

---

[206] The fur from the legs of reindeer, maral, and elk—the so-called "kamus"—is used to line the lower surface of taiga skis. This facilitates their movement and prevents them from slipping backward ("kamus" are fixed with the hair directed backward). Elk "kamus" is particularly strong.

[207] In winter frosts, especially in hazy light, the light-colored legs of the animal on snow are very poorly visible and during slow movement the impression of a dark-colored animal floating in air is common.

In adult bulls body length reaches 300 cm, height at withers 225 to 235 cm, length of ears about 26 cm, and tail 12 to 13 cm. Weight reaches 570 kg.[208] Antler span up to 150 cm and weight up to 20 kg; even larger antlers have been recorded, however.

Overall length of skull up to 620 mm and zygoma width up to 240 mm.[209] Cows invariably smaller and more slender.

226 Body length of newborn about 90 cm and height at shoulders 70 to 90 cm. Weight 13 to 16 kg. In the first autumn of life the young weigh about 100 kg, which rises to about 200 kg by the end of the first year.[210] (V.H.)

Taxonomy

Genus *Alces* contains only one species.

Geographic Distribution

Alces are distributed in the forest zone, partly in forest-steppes, and the edge of steppe zones in North America, Eurasia, and the Caucasus.

Geographic Range in the Soviet Union

The range in the Soviet Union represents the major part of the range of the species and an overwhelming portion of the range in the Old World. It covers almost all Soviet territory except semidesert and desert regions and the mountains of Middle Asia.

The range of elk is of special interest in some respects. Its major changes over the historic period and the particularly extensive colonization of the animal in the last decade are of utmost theoretical importance from the viewpoint of zoogeography and ecology. Contraction and expansion of a range, movements and pulsations of its boundaries, forms of colonization, occupation of new territories, and several other aspects of general zoogeography are vividly revealed in the distributional history of elk.

---

[208] These data are from Flerov (1952). According to others (Buturlin, 1934; Zhitkov, 1914; Kulagin, 1932) the maximum size of Russian elk is somewhat greater—body length may exceed 300 cm, height at shoulders 240 cm, and weight 620 or even 655 kg (40 poods). These maxima, assuming them to be fairly accurate, represent rare exceptions and pertain mainly to animals of northeastern Siberia, which are particularly large. Some data were collected at the end of the last century when elk at many places were of far greater dimensions than at present.

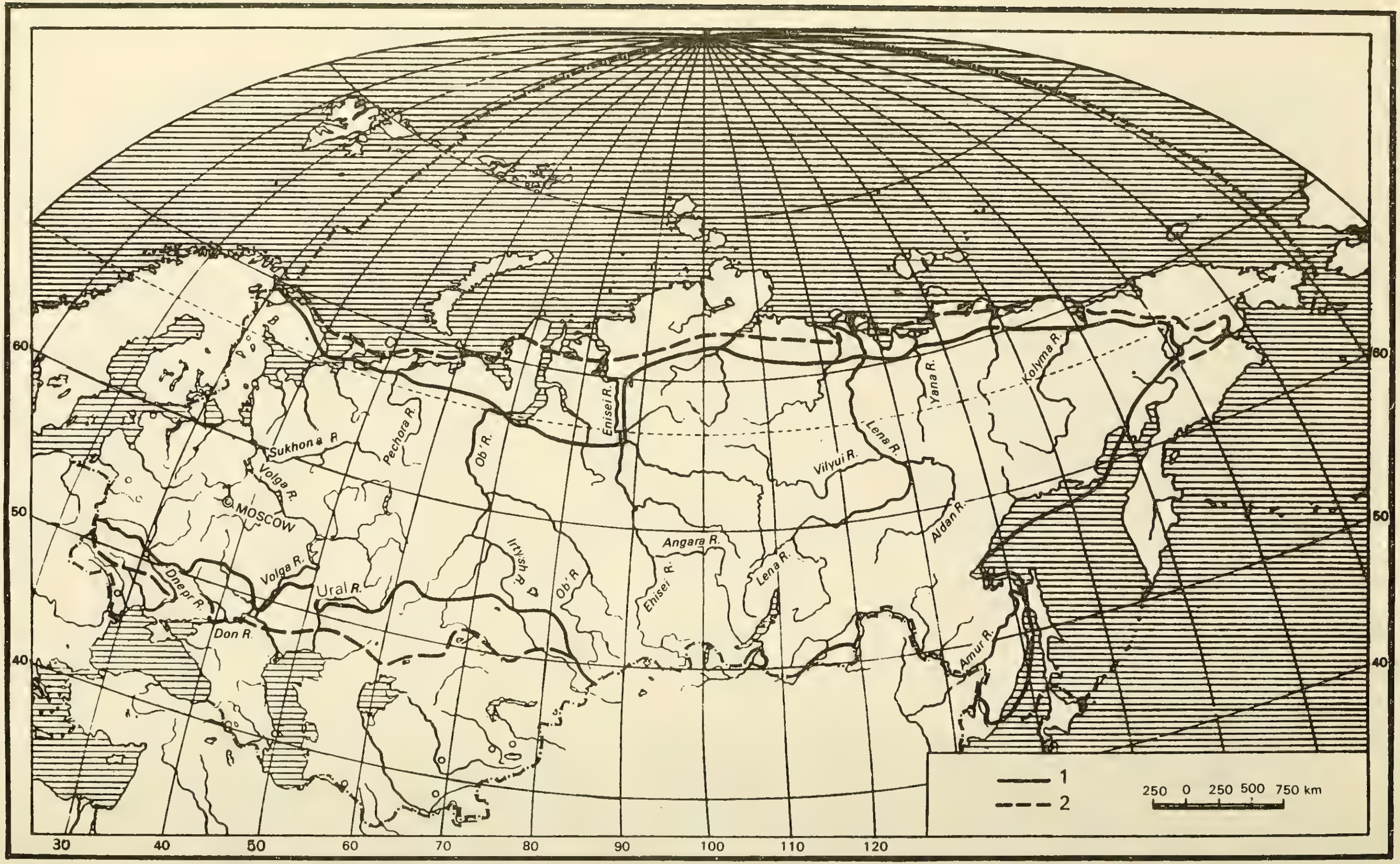
[209] See characteristics of the genus for skull features.

[210] Morphological and morphometric data from Kulagin, 1932; Buturlin, 1913 and 1934; Zhitkov, 1914; Yurgenson, Kaplanov and Knize, 1935; Flerov, 1952; and other sources, including original material.

From an ecological point of view a study of the distribution of elk and the dynamics of their range provide extremely interesting possibilities for delving into the affinity of the animal to a given topographic region, its specialization and ecological adaptability, range expansion into new areas, and several other features, for example, the origin of regular seasonal migrations in an otherwise resident animal. Of special importance is the coexistence of a large ungulate with man in arranging the creation and development of cultivated landscapes.

A study of the range of elk is also of practical interest. Elk is an important species of commerce and represents one of the most prominent objects of hunting in the world fauna. The prospects for utilizing it for these purposes are extremely good. The fate of elk and changes in its range are of exceptional interest from the point of view of conservation. It can be confidently stated that there is no other large animal whose conservation despite all handicaps has provided such extensive and amazing results. Even though many other species facing extinction have been successfully conserved and their population and range enlarged, achievements have nowhere attained those in the case of elk. The results of elk conservation are only comparable to those achieved with saiga antelope (see below). From experiments conducted outside the USSR the effect of conservation of elk can be compared to some extent only to that achieved with the Pribilov fur seal herds. However, in the latter all the prerequisites of success were relatively simple. The same can be said for the conservation of Russian sable.

The view that elk represent typical inhabitants of dense forests, with a preference for swampy taigas, and to a lesser extent mixed taigas in dense forests, prevailed for many years. Similar views were expressed about its range. In the last decade historical and archaeological finds have shown that elk lived far from true taiga. They
228 were extensively distributed not only in the zone of mixed and deciduous forests, but in the forestlands of forest-steppes and in bottomland deciduous forests, and even extensively dispersed in the steppe zone. It has also been established that elk inhabited the montane forests of the Caucasus comparatively recently.


60
50
40
30
40
50
60
70
80
90
100
110
120
Sukhona R.
Pechora R.
Ob' R.
Enisei R.
Yana R.
Kolyma R.
Lena R.
Vilyui R.
Volga R.
MOSCOW
Aldan R.
Irtysh R.
Ob' R.
Angara R.
Enisei R.
Lena R.
Volga R.
Ural R.
Dnepr R.
Don R.
Amur R.
1
2
250 0 250 500 750 km

Nearly 40 years of legal conservation have further revealed that elk, long regarded as a species facing almost total extinction and shy of man ("fugitive from civilization") are, in fact, animals of high vitality capable of extensive distribution. In the absence of direct persecution elk are capable of living, and do so, in the immediate proximity of man in densely populated areas and the environs of large cities.[211] Elk can even be designated somewhat "anthropophilous". Nevertheless they are very readily susceptible to extinction.

Right now, with the population and its density having risen greatly and standing high almost everywhere, the range of elk has notably enlarged. As in the distant past, the animal once again inhabits forest-steppes, has penetrated even the steppe zone, entered the forest-tundra, and even the tundra in the north. This confirms well a characteristic of elk, established on the basis of a study of its former distribution, that ecologically it is an extremely adaptable eurytopic species and not a strictly stenotopic inhabitant of taiga. The confinement of elk to dense taiga may be regarded as mainly due to human persecution. While this zone can be considered an ecological refuge of the species, it is nevertheless quite clear that it does not represent an optimum environment for them.

As far as the range of elk and its dynamics are concerned, dense, tall forests are less favorable than sparse forests with meadows, swamps, and burned-over and felled forest sections. Such areas ensure important winter food-shrubs and twigs. Burned-over and felled forest sections, overgrown with deciduous species, mainly aspen, are particularly favorable in this respect.

Parallel to conservation, such habitats are one of the important factors determining the expansion of range and growth of elk population. Extensive and often continuous felling in the last decade over much of the range of elk radically altered the forest landscape into a zone favorable for its habitation. Herein lies one of the vital factors responsible not only for the rise of population but also for the "anthropophilous" character of elk.

In this connection it is very significant that in western Siberia the

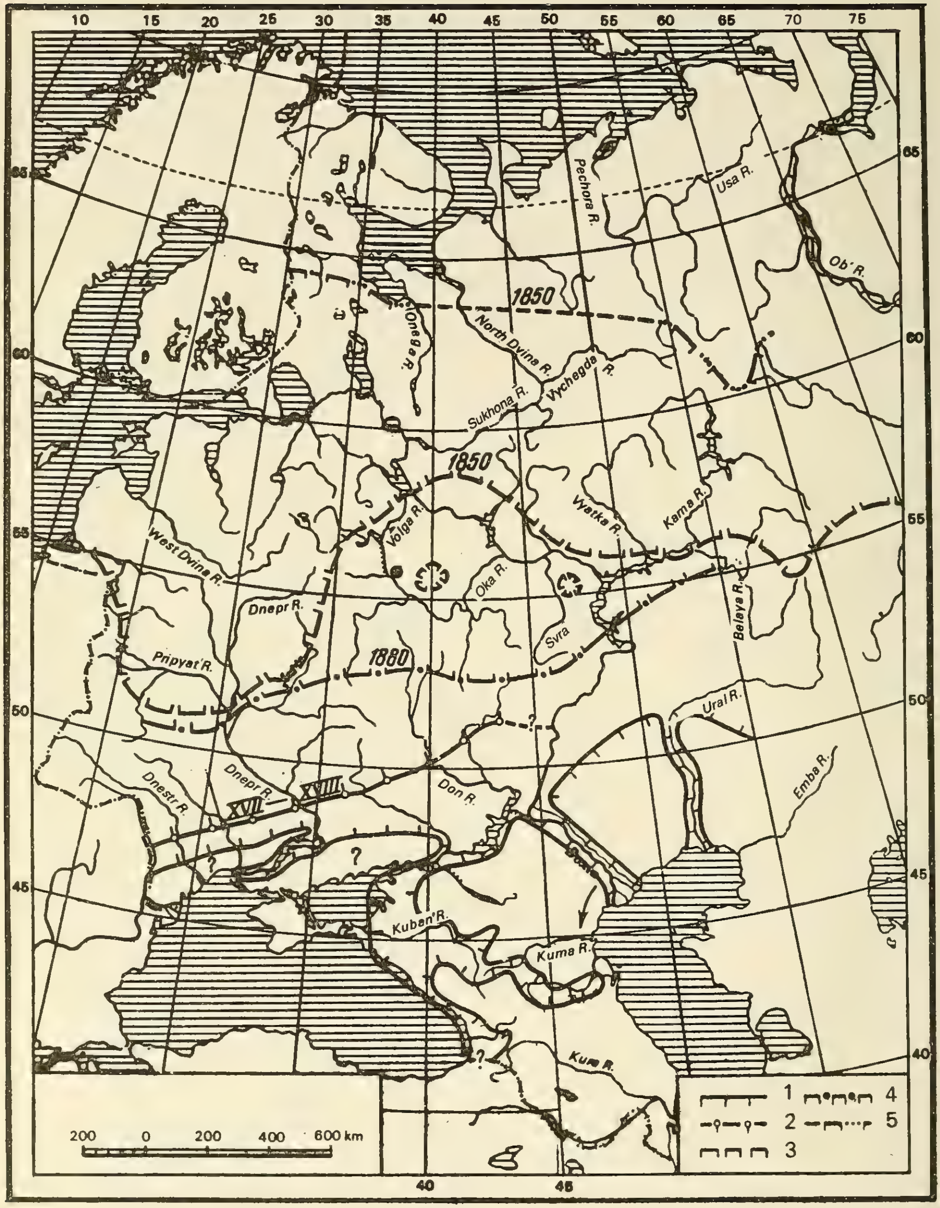
---

[211] Since the 1950's elk have been sighted often in the environs of Moscow and especially Leningrad, where they are sometimes held in, and live around, parks.

---

227 Fig. 70. Geographic range of elk (*Alces alces* L.) in the USSR in mid-1950's (scale in km).

1—boundaries of region of permanent habitation; 2—boundaries of regions of visitations. For details see subsequent maps. V.G. Heptner.


10
15
20
25
30
35
40
45
50
55
60
65
70
75
65
60
55
50
45
40
Pechora R.
Usa R.
Ob' R.
1850
Onega R.
North Dvina R.
Vychegda R.
Sukhona R.
1850
Volga R.
Vyatka R.
Kama R.
West Dvina R.
Oka R.
Belaya R.
Dnepr R.
Sura
Pripyat' R.
1880
Ural R.
Emba R.
Dnestr R.
Dnepr R.
XVII
XVIII
Don R.
?
?
?
Kuban' R.
Kuma R.
Kura R.
?
200
0
200
400
600 km
1
2
3
4
5
40
45

population density of elk reaches the highest level in the southern zone where taiga is sparse and acquires some forest-steppe features (I.P. Laptev, 1958). It has been shown (Sludskii, 1953; and others) that, in the past (eighteenth century and before) elk were abundant in the forest-steppe and a common animal. Thus the widely prevalent view that elk is a northern species cannot be justified.

A characteristic feature of elk, judged from some data collected over the last two-and-a-half centuries, is that its range changed extensively over a comparatively short period (contraction and expansion) and the boundaries shifted over long distances. In some cases and for certain parts of the range the reasons for these rapid fluctuations—usually man-induced—are quite clear, while elsewhere the causes of the phenomenon are not known. On the whole this phenomenon has not been thoroughly studied and is understood only for part of the range (European part of the USSR and western Siberia). However, there is reason to believe that this phenomenon was quite widespread not only in a territorial sense, but also in time.

Different sections of the range over the historic period are described below.

229 *Geographic Range in the European Part of the USSR*

Reconstructed range and range in seventeenth and eighteenth centuries. The range in the period of its maximum distribution (Fig. 71) covered almost the whole European part of the USSR, the forest-steppes, and much, if not all, of the steppe zone.

On the basis of the few historical records available the southern boundary of the range of elk was probably as follows. Commencing in the west at the boundary of Russia southwest of Kishinev, from slightly south of this town, it crossed the Dnestr and went to the Bug

230 Fig. 71. Some changes in boundaries of distribution of elk (*Alces alces* L.) in the European part of the USSR over the historic period and up to the twentieth century (scale in km).

1—reconstructed southern boundary of region of fairly permanent habitation over historic period. Individual transgressions evidently extended beyond this zone. Boundaries in the Caucasus simplified (for more details see Fig. 73). Arrow indicates probable migration from Volga into Kuma; 2—probable position of southern boundary in seventeenth and eighteenth centuries; 3—southern boundary around 1850, the period of utmost recession before mass colonization of elk in the south in latter half of century. Some individual pockets of habitation falling south of the northern boundary shown (Koppen, 1883); 4—probable northern boundary at time of its maximum recession to the south in the middle of the nineteenth century (around 1850); 5—southern boundary of advancement of range southward during latter half of the nineteenth century (early 1880's; Koppen, 1883). V.G. Heptner.

somewhere in the region of Voznesensk. From there it proceeded to the Dnieper in the region of Dnepropetrov (probably even more south) and proceeded toward the Northern Donets, probably in the region of Izyum. Later, it evidently proceeded along the Donets to Don and descended along the latter to the Sea of Azov. The range also covered the Don valley above the mouth of the Northern Donets. Evidently in the region very close to the Don and Volga the boundary bypassed on the north the semideserts on the right bank of the Volga and crossed to the Volga; the range descended thus in the form of a narrow extension along the Volga valley down to the Caspian Sea.[212]

The range (zone of permanent habitation) evidently did not cover the zone of arid steppes and semideserts between the Volga and Ural [rivers]. From the Volga valley the southern boundary crossed to the Ural valley, probably roughly along the line from Stalingrad to Ural'sk, following the northern boundary of the semidesert. The range descended south along the Ural valley in the form of a projection. The maximum distribution of the species is not known but the possibility is not ruled out that it extended to the sea.

There is no doubt that in the forest-steppes of long ago, with innumerable large forest massifs and multiple small ones, elk were distributed widely and fairly uniformly. In the steppe region, however, the range was not continuous. Elk were confined to some individual forest massifs and to bottomland deciduous (gallery) forests along rivers which cut into the steppes. There is no doubt that elk were thus not distributed exclusively along the Don and Volga. We can assume they were widely distributed south of the line shown [map] between the Danube and Don. They evidently reached the sea through valleys of not only large rivers such as the Dnestr, Bug, and Dnieper,[213] but also along much smaller rivers such as Molochnaya, Mius, and others, on which also there were bottomland deciduous forests in the distant past. Indubitably they emerged into open steppes for grazing while moving from one island to another, and during migrations were generally confined to open steppes which, in olden times, were far richer in tree and shrub food than in the Recent period. A similar picture is currently seen in Kazakhstan and the Trans-Volga where the animals not only perform major migrations (up to 100 km) across open steppes but also enter semideserts. There is every reason therefore to assume that the range of elk between the Danube and Don extended up to the shores of the Black and Azov Seas. It is highly possible that even in Trans-Volga its boundary lay more southward and Uzen' also fell within the range.

---

[212] According to Kirikov (1955) and unpublished data furnished by S.V. Kirikov and N.K. Vereshchagin.

[213] Elk have been reported in the lower courses of the Dnestr (Kirikov, 1955; map) at Ol'vinsk on the shore of the Bug estuary (1000 A.D.) and on the shore of Kuyalnits estuary (Il'insk, 1000 B.C.; Pidoplichko and Topachevskii, 1953).

The situation described above prevailed in the historic past, probably in the early part of the last millenium and at places later, probably up to the sixteenth or even seventeenth century. Information is available about the occurrence of elk in the lower course of the Don from 800 to 1000 A.D. (ancient township of Tsimlyansk). It is possible that the range was just as extensive, or almost so, even at a much later period. Pallas has written (1811) that around 1800 elk thrived throughout Russia from the White Sea to the Caucasus, i.e., evidently lived even in forest-steppes and steppes.

231 There is no information whatsoever about the northern boundary of the natural range over the historic period. Undoubtedly, however, it could not have been farther removed than the boundary at the middle of the present century, i.e., the southern boundary of the tundra and the sea coast (see below). This supposition is nonetheless tentative.

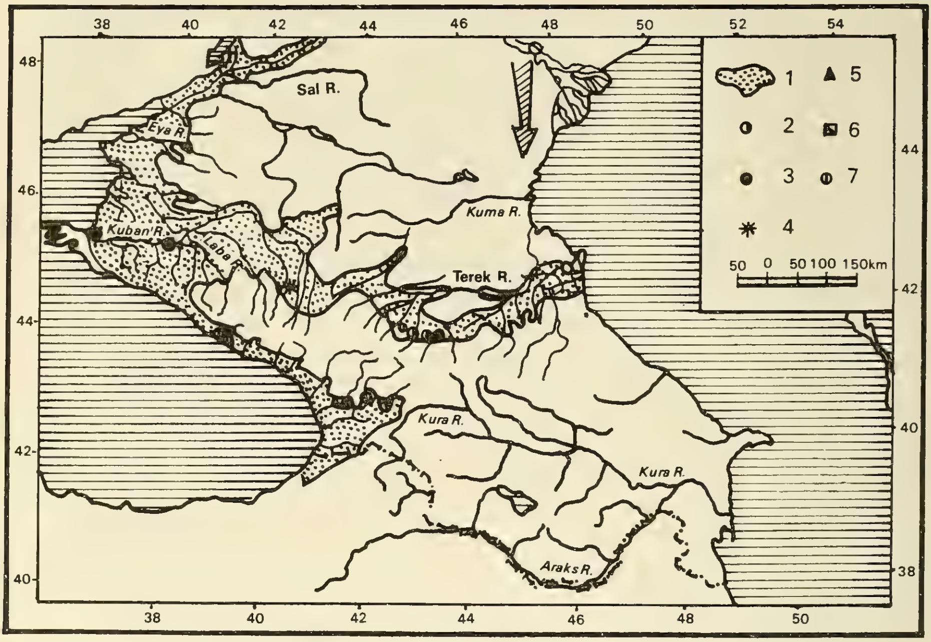
In the seventeenth and eighteenth centuries the boundary evidently passed along the northern part of the steppe zone or along the southern rim of the forest-steppe. From Moldavia to the Northern Donets it deflected slightly north or generally corresponded to the previously mentioned Kishinev-Voznesensk on Bug-Dnepropetrovsk-Izyum on Northern Donets line. Elk were present even in the Black Forest at the watershed between the sources of Ingul and Ingul'ts (about 1740), and below Izyum (about 1667). However, to the east the range boundary rose considerably northward, crossed the Don at about 50° (Boguchar region), and ran along the Khoper in the Novokhopersk region or slightly more southward (elk were present in Tellermanov Grove around 1657).[214] From there the range boundary proceeded toward the Volga, probably straight eastward. It is highly possible that in the forests of the Khoper and Medveditsa elk were present even more southward. No information is available on the Trans-Volga region.

In the Caucasus (Fig. 72) the region of elk occurrence adjoined the Russian plains.[215] A connection occurred through the lower

---

[214] According to data of S.V. Kirikov.

[215] The first reference to the presence of this species in the Caucasus is found in Pallas' works (1811). He states that elk were present "omnique Rossiam, a Mari Albo



232 Fig. 72. Former distribution of elk (*Alces alces caucasicus* Ver.) in the Caucasus (scale in km).

1—probable range in historic period; 2—references in literature for the early nineteenth century; 3—dzvars in which elk were found; 4—habitations on Urup River; 5—kitchen middens of eighth to thirteenth centuries; 6—remains of fourth to first century B.C.; 7—Upper Palaeolithic remains. Arrows indicate probable courses of colonization and migration of elk in the Caucasus (original by N.K. Vereshchagin, simplified and with supplementary information from S.V. Kirikov). V.G. Heptner.

course of the Don and the Azov region of the northern Caucasian steppes. More to the east, where dry steppes and semideserts lie, no permanent linkage of the range is evident. However, it is wholly possible that the animals migrated along the Caspian Sea (from the Volga estuary) but due to the recession of the southern boundary of

usque ad Caucasum". Considerable controversy ensued but by and large Pallas was deemed wrong (see Koppen, 1883; Dinnik, 1914; Satunin, 1910; and others; more recently, Kulagin, 1932). The former occurrence of elk in the Caucasus was conclusively proved however by N.K. Vereshchagin and O.I. Semenov-Tyan-Shanskii, 1947. They found elk skulls in Ossetian dzvars [ritual sites] at Lezgor and Digorized in Urukha River basin (Vereshchagin and Semenov-Tyan-Shanskii, 1948; Vereshchagin, 1948; Vereshchagin and Naniev, 1949; Vereshchagin, 1949). In the light of these data not only the assertion of Pallas but also data from other early authors, such as biologists (Gmelin, Georgi, Clark, Middendorff), as well as hunters (Polferov, 1894), and references in Ossetian folklore have acquired special significance.

the range in Volga-Don region, described above, this continuity was interrupted.

Outlines of the Caucasian elk range can be reconstructed only in an extremely tentative form, largely hypothetical, and only for the last century. Elk evidently lived in the steppe parts adjoining the Sea of Azov where reed thickets were abundant and bottomland deciduous forests were present not only in the Kuban delta but also along streams flowing into the sea. Later the animals moved into the whole of the forested western extremity of the mountain range and the forests on its northern slope and foot-hills. In the past these forests penetrated far into the plains and were closely associated with forests lying on the Stavropol highlands. In the east elk probably lived on the plains, in forests of the Terek basin, and in the lower reaches of the rivers their range probably reached, or almost reached, the Caspian Sea.

In the Trans-Caucasus the range of elk extended in the form of a belt along the Black Sea coast and slightly enlarged in the basin of the Rion and other rivers of this part of the country without, however, reaching the Kura basin. The possibility is not excluded of the range crossing slightly into Turkey in the region of the lower reaches of the Chorokh or still more southward.

The range described above is that of the fifteenth to the early nineteenth centuries. Elk were extensively destroyed in the Caucasus in the seventeenth and eighteenth centuries and consequently the range shrank notably. The last elk, judging from skulls in the sanctuaries of the central Caucasus, were probably killed in the early nineteenth century. In the lower reaches of the Kuban, between the main channel and the tributary at Kalaus village, elk were sighted even in 1800 (Clark 1810; cited by S.V. Kirikov) and evidently were not exceptionally rare there.[216]

The period of penetration of elk from the north into the Caucasus should perhaps be placed at the very end of the Pleistocene. In the Upper Palaeolithic period elk were evidently dispersed within the region described.[217] In the lower Don at Tsimlyansk elk remains were found in the ancient township dated 800 to 1000 A.D. (they were absent in Sarkela from 900 to 1100 A.D.). It is difficult to state precisely when the contact between the Caucasian and northern range was broken. Apparently it occurred at the commencement or in the first half of the last millenium. This is borne out by the taxonomic isolation of Caucasian elk, which represent a different subspecies. Furthermore, there has never been a full merger between Caucasian and Russian populations. This also may have influenced differences in the morphology of the Caucasian form.

---

[216] Two young elk at Kalaus were extremely tame; Clark (1810) was informed that many wild elk could be seen in the steppes in spring.

[217] The elk range in the Caucasus is based on articles cited before and on the unpublished data and map of N.K. Vereshchagin.

Range in nineteenth and twentieth centuries. In the first half of the nineteenth century a very sharp, almost catastrophic reduction in the range of elk occurred and its southern boundary receded far north. Compared with the boundary line shown for the 1700's, by the mid-1800's the boundary had shifted at places 450, 600, or even 1,000 km. Recession was particularly far in the central regions and less in the west and east.

233 By 1850 the southern boundary of the elk range in the European part of the USSR formed an irregular line running roughly through the following places: mouth of the Neman, upper course of the Pripyat, middle course of the Sluch, mouth of the Pripyat, upper course of the Desna, Kalininsk, Rybinsk, Bui (northernmost point), lower course of the Unzha, middle course of the Vetluga, the Volga east of Vetluga mouth, region of the mouth of the Vyatka, mouth of the Beloe, middle course of the Ufa, sources of the Ufa and Ural [river], and eastern slope of the Urals [mountains] at roughly 56° N lat. Outside this boundary (south of it) there were two small islands of habitation of elk, east of Moscow in the forests of Vladimir district and between the lower courses of the Sura and Volga north of 55°. Other pockets in which elk survived could also have existed (Köppen, 1883; boundary description as depicted in Köppen's map).

In the nineteenth century a notable southward recession of the northern boundary occurred, which chronologically coincided with a similar phenomenon along the southern boundary, already described, for the first half and middle of that century. The northern boundary in the west (Karelia) at that time ran roughly between 64 and 65° N lat. and in the east proceeded from the source of the Vychegda, passed to the south of the Pechora basin and descended southeast almost to 60°, intersected the Urals there, rose slightly northward passed to the north of the Sosva, and ran into the upper Lozva (Nasimovich, 1955). Distribution in the area between White Sea and the source of Vychegda is not known. This depression of the northern boundary of the range was associated with the corresponding phenomenon in Siberia (see below).

Thus by the middle of the century the range of elk had shrunk sharply because of the extremely pronounced shrinkage of the southern boundary and to a lesser extent of the northern boundary as well, which compared to the period of maximum enlargement lay at places even 500 to 600 km more southward.

The reasons for this reduction in range are not clearly understood because they were inadequately studied. The human factor (hunting), of course, played a significant role. According to some authors (Nasimovich, 1955) it was the decisive factor.[218] However, it does not seem credible that this factor alone could have caused the extensive shift of boundaries which occurred fairly synchronously over an immense expanse from the Baltic region to the Urals, and farther to the east, a shift which compelled the animal to move out of an extensive territory extremely favorable to its survival. The chronology of this phenomenon has also not been traced completely. It is difficult to state when it commenced but without doubt it developed over some decades and the boundary described formed as a result of steady change which was apparently quite rapid. In any case, at several places where elk were formerly quite common the local populace and even hunters had forgotten this animal by the middle of the century. When later a southward advancement of elk began anew, quite often, for example in some parts of Simbir province (Ulyanov district), it was a totally unknown animal to the local people.[219] In the historical perspective of the species (even over the last few centuries), the range shrinkage described above should be considered rather rapid. This was a spontaneous "compression" of the range with very few parallels.

234 After 1850, when the contraction of the range had evidently reached maximum, reenlargement commenced in the south. Elk began reappearing in places where they had been absent for several years. Animals from northern forests often settled down at fairly long distances from their original habitats. They colonized new places and multiplied, often quite rapidly. Population increments were due not only to reproduction, however, but also the arrival of new

---

[218] The main reason for the intense persecution of elk in the first half of the last century was not the animal's meat. Under sparse population conditions it was of no commercial importance. Hunting of the animal was stimulated by the use of elk hide by the Government which, commencing from the time of Peter the Great, used them in uniforms for some regiments and elk chamois in riding breeches and jackets. The use of elk hide finally ceased in the nineteenth century because of the sharp reduction in population and range of elk. At the commencement of the twentieth century only one guard regiment was outfitted in a uniform made from elk hides and that, too, for ceremonial purposes only.

[219] Incidents of occurrence of European bison in B. Nizhegorod province reported in literature in the middle of the last century evidently relate to captures of elk. At that time elk were so rare in the province that the local people did not recognize them and, having forgotten the name "elk," called these animals "builo" [a type of bison] (Koppen, 1883).

groups of animals in considerable numbers.

The southern boundary of the range advanced eastward and westward over relatively small distances, up to 100, 150, and 200 km, but in the central regions up to 500 to 600 km. By 1880 it ran roughly along the following places: upper reaches of the Sluchi and Dnieper slightly north of Kiev, Chernigov, Desna, slightly south of Bryansk, slightly north of Orel, upper reaches of the Voronezh, slightly north of Tambov, slightly south of Penza, slightly south of Ulyanov, and lower reaches of the Beloe (Köppen, 1883; the above line is based on Köppen's map). Southward advancement of elk continued even later, in the 1880's and the 1890's to a lesser extent. At that time the population of the animal in colonized regions also increased. Finally, by the early twentieth century elk had become quite common at many places and were even abundant in some (B. Simbir province). Data concerning these phenomena are quite sketchy, however.

The southward movement was rapid, more rapid and more perceptible anyway than the boundary recession. At some places colonization was evident and rapid because of migrations over long distances and the unexpected appearance of the animals; fairly large numbers appeared suddenly in some areas (Alatyr basin, Simbir province, now Ulyanov district).

The reasons for the foregoing phenomena are not clear. It is possible that an intense felling of forests in the central provinces, commencing after the agitation of local landholders in the 1860's (abolition of land rights in 1861) played an important role. These felled clearances led to the formation of large areas with young saplings, i.e., to the formation of an environment extremely favorable for elk. This, however, could not have been of decisive importance and at best would only have influenced its course in some individual limited sections. The environment in the southern forest zone had always been favorable for elk. Moreover, at many places a significant number of elk appeared even in the absence of such clearances under conditions which did not at all vary from the original ones (forest along the Sura River).[220] Evidently the settlement of elk in the south was stimulated mainly by conditions prevailing in regions from where migrations took place. There is no doubt that the colonization of elk in the south must have been preceded by a significant increase in their population in the north. It is possible that forest fires compelled elk to move out from some regions.

---

[220] These and other data cited above for Simbir province were communicated to the author by S.A. Buturlin some time ago.

Range at commencement of twentieth century and in the 1920's. Information is inadequate for precisely demarcating the boundaries of the elk range in the early twentieth century. By then the southern boundary corresponded fairly well to that described for 1880. In the upper reaches of the Don and Oka, and probably also at other places, it possibly lay somewhat more northward; in other areas it may have occupied a more southern position (Trans-Volga, Ural, and probably in the west). In any case, early in the century elk were widely dispersed in the forest zone and reached quite far into the south. Their population was fairly high, for example in the provinces of Vladimir and much of Ryazan' and Moscow as well. There the animals lived in forests directly adjoining Moscow, which are now markedly reduced (Pogonno-Losin Island, Novogireevo, and Losin Island; V.G. Heptner). This was the situation until the mid-1910's.

235 At the end of World War I and in the years of the Civil War the elk population was drastically decimated by unrestricted poaching. In much of their range in the European part of the USSR elk became rare and faced total extinction. Banning of elk hunting, decreed in the very first year of the Revolution, exerted some influence only by the mid-1920's. The southern boundary of the range again receded greatly northward. The southern boundary of the range in this period of maximum depletion has not been established. It is fairly well known for 1928, when some signs of restoration of the elk population were observed or, more correctly, population reduction and decrease in the range were checked. It is even possible that at some places the range enlarged somewhat, of course very imperceptibly, and the 1928 line can generally be considered close to the boundary of utmost depletion of the range in the 1920's.

This boundary (Yurgenson, 1935; Danilov, 1951) commenced in the west at the former Russian state boundary, slightly east of the lower reaches of the Sluchi, and ran east slightly north of 51° N lat. Short of 30° E long. it turned steeply north, later west, passing to the west of the Minsk district, and again turning east crossed the upper
236 reaches of the Berezinsk. From there it again turned north, left much of the upper reaches of the Western Dvina out of the range, and running southeast crossed the very source of the Dnieper. Farther away, forming a narrow loop southeast of 35° E long. (toward the Volga) it turned sharply southwest and, describing an arc, crossed the Desna twice—initially at its source (southwest) and later in Bryansk region or slightly south of it (on the east).

From this place the boundary line turned initially northeast and crossed the Oka slightly southeast of Kaluga; later it proceeded slightly north of the Oka and left the Oka roughly at 55° N lat. (slightly north of the mouth of the Moksha). From there the range formed a long and narrow extension along the Tsna southward roughly up to Tambov. The eastern boundary of this extension ran through the midcourse of the Moksha in the vicinity of the mouth of the Oka. Between the mouths of the Oka and Sura the boundary ran slightly short of the left bank of the Volga. From there the range formed a large triangular projection to the south. Its western boundary ran initially along the Sura and later left toward the interfluve region of the Volga and Sura, slightly north of the source of the Sura; the eastern boundary from there turned toward the Volga north of Ulyanov. Later, the boundary proceeded initially southeast and then north toward the mouth of the Beloe to Kam. Continuing farther, initially somewhat northward along the left bank of the Kam, it later turned east steeply and, crossing the upper reaches of the Ufa, ran northeast into Siberia through the source of the Chusovoi.

The northern boundary of the range in these years, as in the much earlier period, is very poorly known and can only be drawn tentatively. In the Kola peninsula elk were evidently not distributed in the north beyond the forest boundary and did not enter the forest-tundra toward the Barents Sea.[221] Toward the White Sea in the east the boundary probably extended up to the latitude of the arctic circle. Thus elk were encountered in the southern half of the peninsula. On the mainland the northern boundary apparently extended along the shore of the White Sea and probably reached, or almost reached, the lower reaches of the Mezen'. The range encompassed the entire basin of the middle and upper reaches of that river. In the Pechora basin the range boundary descended sharply southward and evidently went around it to the west and crossed somewhere in the upper reaches, probably around 62° N lat., running toward the Urals at 61° to 62° N lat.[222]

[221] Around 1930 the boundary ran roughly along the Ponoi, crossed mid-course of Vorona, and ran across the Pulozero at Notozero (Semenov-Tyan-Shanskii, 1948).

[222] The boundary of the elk range in the Pechora basin and some parts of the Urals underwent considerable changes in the last century. Sometimes it moved northward and at other places significantly southward, until elk appeard on the Pechora only as transgressors. The animal population also fluctuated sharply.

In the Pechora basin the boundary fluctuation in the last century was evidently associated very little with the extinction of the animal and depended more on the condition of food sources (availability of young saplings of deciduous species). Animals moved from this region and colonized elsewhere. Because of scanty information it is not possible to draw a satisfactory chart of the phenomenon (some data are provided by Teplov and Teplov, 1947; and Nasimovich, 1955).

Geographic range in 1930's and 1940's and present boundaries. Following the range contraction described above, a gradual, initially very weak and later increasingly rapid expansion, occurred from the end of the 1920's and at some places probably somewhat earlier. It proceeded south and partly north and northeast (Pechora basin and the Urals). This phenomenon is the result of planned conservation and attendant increase in population. In the European part of the USSR from 1920 through 1950 elk increased roughly 15 to 20 times (Danilov, 1951; see "Biology" below).

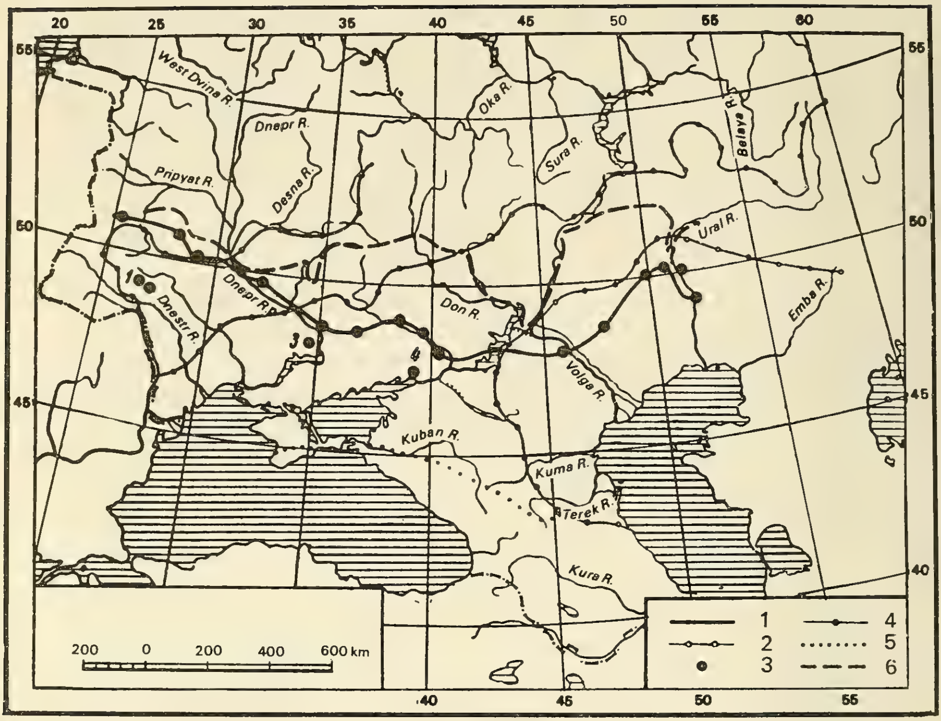
The southward expansion of the range in the European part of the USSR proceeded at the rate of 200 or even 400 km over 18 to 20 years. On the average the boundary there in those years advanced by 120 km and the range enlarged southward by over 400,000 km.^{2} Thus in the 1930's and 1940's the range in the forest zone was reestablished, completely colonized, and animal density quite high. From the 1940's colonization of forest-steppe zones commenced and pene-
237 tration into steppe zones was observed at places; some animals moved even into the semidesert zone.[223]

By 1947 the southern boundary of the range had undergone the following more important changes. The area of the above-described northward curve of the boundary into the basin of the upper Dnieper and upper reaches of the Western Dvina was greatly reduced in the west. Its northernmost point lay roughly in the Mogilev region. In the region between the Desna and Tsna the range on the

---

[223] The occupation of new places by elk was initially in the form of occasional visitations by isolated animals which later increased both in number of animals and frequency of visitations. The animals gradually settled in the new place and began multiplying. In the forest zone this process was hardly perceptible; transgressions were usually over small distances and advancement of the range southward very gradual. During the occupation of southern zones—forest-steppes and steppes—occasional transgressions were also observed, usually in "spurts" over long distances (for example, tens and hundreds of kilometers in the open steppes). The animals often happened into a totally inhospitable environment (sometimes in a town) and usually died. Gradually these visitations became increasingly frequent and some animals, finding fairly suitable conditions (islands of forest in the steppes), settled down. Sometimes colonization occurred in alien zones—steppes, semidesert, tundra, along bottomland deciduous forests and groves, and even shrub thickets.

At some places regular seasonal (summer) migrations of elk into tundra occurred and the animals were sometimes trapped into wintering at places north of the region of permanent winter residence. As a result of these factors it is difficult to distinguish the region of permanent habitation from the region of transgressions in several cases over large territories, all the more so because the process of occupation of new areas is still continuing. Expansion of the range of elk and the mode of expansion are of considerable theoretical interest for understanding the phenomenon of colonization in general.


20
25
30
35
40
45
50
55
60
55
50
45
40
West Dvina R.
Dnepr R.
Oka R.
Sura R.
Belaya R.
Pripyat R.
Desna R.
Ural R.
Dnepr R.
Dnestr R.
1
2
3
4
Don R.
Emba R.
Volga R.
Kuban R.
Kuma R.
Terek R.
Kura R.
200
0
200
400
600 km
1
2
3
4
5
6

238 Fig. 73. Southern boundary of distribution of elk (*Alces alces* L.) in the European part of the USSR in 1958 (scale in km).

1—southern boundary of region of fairly permanent habitation; 2—southern boundary of region of visitations from 1955 to 1958 (in Trans-Volga some transgressions which took place in the very early years have also been taken into consideration). Circles on line represent some important definite points referred to in the text; 3—points of particularly distant visitations (1—Gorodok region; 2—Solobkovet region; 3—Novopokrov region; 4—Sambek). Question mark on Ural River indicates that elk probably spread farther south; 4—southern, western, and part of northern boundary of forest-steppe region; 5—southern boundary of steppe zone in the Crimea and the Caucasus; 6—northern and western boundaries of semidesert and desert zone. Boundaries of natural zones shown schematically from data of S.V. Kirikov. V.G. Heptner.

whole advanced somewhat southward, and that too very insignificantly. But then, between the Tsna and Volga and along the Volga the boundary shifted southward very extensively, although not entirely uniformly. The curvature of the boundary in the north between the Tsna and Sura almost disappeared and the boundary descended along the Volga almost to Saratov. The entire boundary advanced particularly extensively in the south into the Trans-Volga and Urals. By 1947 it had already extended from Samarsk Luka to the southern Urals, where it stopped only slightly short of the Ural River valley in its meridional course.[224]

The southward advancement of the boundary, compared with the 1928 position, was 100, 200, or even 500 km at some places. At other places, contrarily, it did not advance at all. This was particularly so at places where the range had reached the natural topographic boundary even before, but primarily where further advancement was hampered by human intervention (some details of the boundary are shown in Fig. 74).

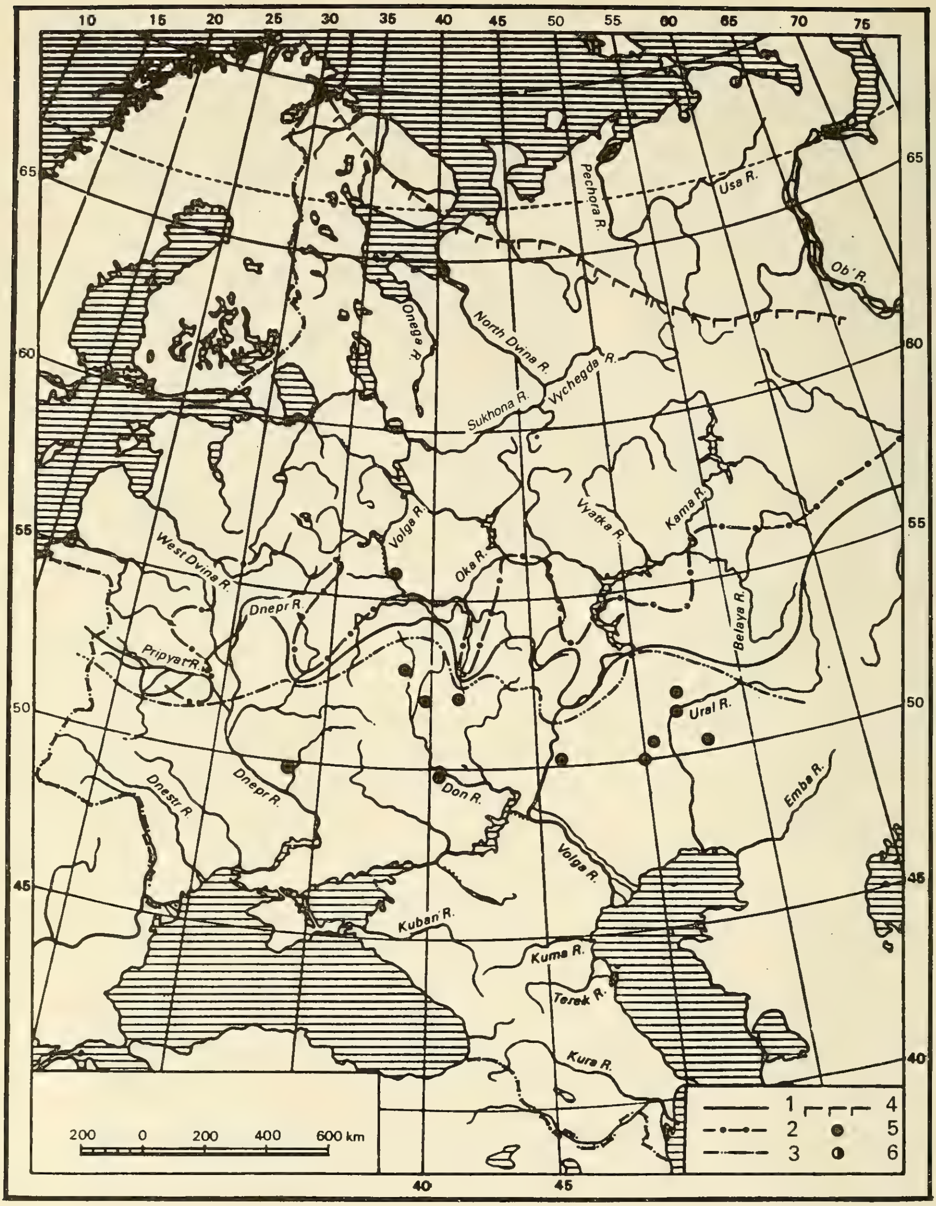
Adequate information is not available about the northern boundary of the range of elk in the period under description (1928 to 1947). It is known, however, that the population of the animal increased even in the north and the range enlarged in that direction also. In the northern Urals, by that time, it evidently reached 65° N lat. or approached it. Probably the advancement in the Pechora basin was also roughly of the same magnitude or slightly less.

After 1947 the elk population and its density in the European part of the USSR continued to increase and the southern boundary of the range continued its progressive advancement southward. The animals occupied an increasingly greater area of the forest-steppe zone. By 1952 elk in the Urals descended so far southward that they colonized not only the entire mountainous district, but also the Ural [River] valley from Orsk to Orenburg (55° E long.) and extended southward even beyond the river.

In 1952 the southern boundary of fairly permanent habitation of elk in the European part of the USSR traversed from Orenburg through Buzuluk Bor to Kuibyshev to the Volga and farther down along the river roughly to Saratov. Along the left bank of the Volga in this section elk were encountered on the Chapaevka River (Mocha) above Chapaevska, i.e., south of Kuibyshev and in the valley of the Great Irgiz opposite Vol'sk (west of Gmelinovka station; Martynov, 1951; Stroganova, 1951). From Saratov the boundary ran southwest to Shirokii-Karamysha on the Medveditsa at the southern boundary of the Saratov district and from there up along the river toward Petrovska and then to the west toward Rtishcheva and
239 Makarova. It then turned upward along the Khoper to the Penzena district and later along the Tsna basin in the south almost to Tambov. From there the boundary proceeded toward Ryazan', through the source of the Don at Orel, then to the southwest toward the

---

[224] The boundary of distribution of elk in 1947 is based on data from D.N. Danilov, 1951.


10
15
20
25
30
35
40
45
50
55
60
65
70
75
65
60
55
50
45
40
Usa R.
Pechora R.
Ob' R.
Onega R.
North Dvina R.
Vychegda R.
Sukhona R.
Volga R.
Kama R.
Vyatka R.
Oka R.
West Dvina R.
Dnepr R.
Pripyat R.
Belaya R.
Ural R.
Dnestr R.
Dnepr R.
Don R.
Emba R.
Volga R.
Kuban' R.
Kuma R.
Terek R.
Kura R.
200
0
200
400
600 km
1
2
3
4
5
6
40
45

238 Fig. 74. Boundary of geographic range of elk (*Alces alces* L.) in the European part of the USSR and changes in it in the first half of the twentieth century (up to 1952) (scale in km).

1—southern boundary in 1947 (from Danilov, 1951); 2—same in 1928 (from Danilov, 1951); 3—same in 1952 (V.G. Heptner); 4—northern boundary in 1920's; 5—some particularly deep transgressions in the 1930's, 1940's, and beginning of 1950's (1951 and 1952); 6—transgression toward Kara Bay. V.G. Heptner.

midcourse of the Desna and in the north to Roslavl' and Mogilev. From there it turned south to the mouth of the Sozh on the Dnieper and the lower reaches of the Pripyat. Having encompassed a significant part of the southern tributaries of the Pripyat, the boundary continued beyond the USSR frontiers in the Brest region.

The main advancement of the boundary to the south during the years 1947 to 1952 thus occurred in the region of the upper Dnieper. There the great northward curvature of the boundary line, so distinct in 1928, totally disappeared. The boundary moved most extensively in the Volga region, between the Tsna and Volga, and in the Urals. Boundary advancement occurred in other regions also, but to a less extent.

Available information about the northern boundary of the range in 1952 is sketchy. Evidently, however, the region of permanent habitation of the animal at that time reached the northern limits of the forests.

In the 1940's and the commencement of the 1950's there were frequent visits by elk beyond the southern limit described above, often very far beyond. Along the Ural River visitations were recorded up to Ural'sk and Chapaev, in the steppes in the Dzhambeita region (east of Chapaev), in the steppes between Chapaev and Furmanov on the Great Uzen' River (50° N lat.), in the lower reaches of the Eruslan, along the Khoper to Balashov, in the upper part of the Don basin in the Ertil' region (east of Voronezh), in the Lipets, Kulikov and Usmansk forests (left bank of Voronezh, north of the city of Voronezh), and even in the Boguchar region (slightly southeast of 40° E long. and 50° N lat.). There were other distant visitations as well. In the Ukraine transgressions are known in the following districts: Poltav (almost up to Poltava), Sum, Chernigov, Kiev, Kamenets-Podol', Zhitomir, Volyn, and Roven.[225]

The southern boundary of the region of fairly permanent habitation of elk in the Dnieper basin had already reached, or almost reached in 1952 the boundary of maximum range spread in 1880. Some individual visitations were recorded even beyond this line. The boundary lay even slightly more north (by a maximum of 100 km) of the 1880 line at the source of the Oka and in the upper reaches of the Don and Voronezh. The two again coincided at the sources of the Tsna and Khoper. Later, along the Volga and between the Volga and the source of the Khoper (along the source of the

---

[225] Based on data by D.N. Danilov, 1951; Stroganov, 1951; Martynov, 1951; Korneev, 1952; Kirikov, 1952; Shvarts, Pavlinin and N.N. Danilov, 1951; Serzhanin, 1956; V.A. Popov and Lukin, 1949; Sludskii, 1950; Barabash-Nikiforov, 1957; and others.

Medveditsa), the 1952 boundary descended much farther south (by 350 km) along the river than in 1880. The boundary lay that far south (Saratov region) only in the seventeenth and eighteenth centuries. Slightly west of the boundary line for the seventeenth and eighteenth centuries elk were only seen as transgressors (Balashov and Boguchar).

The differences between the 1880 and 1952 boundaries are even more pronounced beyond the Volga: around 50° E long. (Samarsk Luka) the new boundary lay more to the south than before by 100 to 150 km, and then around 55° E long. by 400 km or somewhat more. It should be borne in mind that the 1880 line described above refers mainly to permanent habitations, but partly also indicates visitations, while the new boundary line is confined only to fairly permanent habitations. Transgressions at the end of the 1940's and in the first or second years of the 1950's, compared with the 1880 line, extended to distances (measured along meridians) of 150, 250, 350, 400, or 500 km.[226]

From 1952 through 1958 the population and extent of colonization of elk continued to increase in most places in the European part of the USSR. Furthermore, in vast expanses along the southern part of the range conditions were created for supporting an extremely high density, bordering on overpopulation. As a result, not only were there deep and frequent transgressions beyond the range boundary but also some southward advancement of the region of permanent habitation. It was, however, not of such proportions as in the preceding decade since the entire region favorable for the habitation of elk to the south of the forest zone and in the forest-steppes was
240 already occupied. The animal continued to occupy isolated forest masses along the southern edge of the forest-steppe region. In the Don basin such forests occurred along the Voronezh above the city of Voronezh (Lipets, Kulikov, and Usmansk—partly up to 1952), the Khoper (Borisogleb forest, Tellermanov grove; Khoper preserve in 1952), and some other regions such as forests occurring southwest of Voronezh along the Sosna River, and Khrenov pine forests on the Bityuga River at Khrenovoe. Elk transgressions were noted in the Annen, Bobrov, Novo-Kalitven, Korotoyak, Ostrogozh, and Pavlov regions of Voronezh district. Here the animal was observed even in very small forest sections or even in open steppes far from forests, for

---

[226] The 1947 boundary had already reached the 1880 position at some places. Along the Volga and in Trans-Volga it even crossed it (see map).

example in Dobrin and Bogucha regions (Barabash-Nikiforov, 1957[227]).

Geographic range at commencement of latter half of 1950's and in 1958. In the north elk reached not only up to the northern boundary of the forest, but occupied the entire region of forest-tundra and led a normal and settled life up to the southern boundary of the tundra. This should thus be regarded as the northern boundary of the region of permanent habitation. Elk fully colonized forest-tundra after the 1950's, mainly from 1952 and 1953. Before this they were seen there only as transgressors or lived in small numbers and only at some places (V.Ya. Parovshchikov; Skrobov, 1958 and 1958a).

In summer large numbers of elk migrated deep into the open tundra and colonized it everywhere, reaching the coasts of the Barents and Kara Seas. This occurred in all the tundras east of Kanin Peninsula. Arrivals in the tundra took place in spring (May–June) and at places resembled true migrations. In autumn (September–October) a reverse movement led to wintering in the forest-tundra.[228] While migrating, elk sometimes overcame barriers such as water bodies (rivers and gulfs), for example Korovinsk Bay on the right bank of the Pechora (Skrobov, 1958). The picture of seasonal range expansion on the Kola Peninsula is very clear: in the warm season animals occurred throughout the peninsula up to the sea coast, while in winter they remained only in the forest zone (R. Zakharov).

In forest-tundra elk winter mainly along river valleys overgrown with osier, which serves as their food. Some animals winter even in the tundra zone, having been displaced from open tundra into the floodplains of much larger rivers (Pechora, Om', Pesha, and others), along which narrow strips of osier extend far into the north beyond forest-tundra. Thus elk winter even at the mouth of the Pechora. In winter they are sometimes found as transgressors even in open tundra (known up to 68° N lat.).

On the Kanin Peninsula elk live year-round in forest-tundra in small woods[229] between the Semzha (on the bank of Mezen' Bay) and the Nes'ya and winter even below Chizha where only willow thickets ("ery") are available: in fact, they are so tall that they are never covered by snow. In summer elk are numerous in the open tundra north of the latitude of Chizha, wherever low osier beds exist. The animal reaches the northern limits of the peninsula (Cape Kanin) and the Kanin Kamen' mountain ridge in the north of the peninsula. Along the northern slope of the Kamen' where tundra has a more severe Arctic climate and willows are absent, elk are not seen (E.P. Spangenberg; observations for 1956 and 1957).

---

[227] In the basin of the upper Don colonization was more successful than in other places. The natural conditions there are, of course, more favorable for such settlements (forest regions along the Don, Voronezh and Tsna).

[228] Even massive migrations have been reported (Skrobov, 1958).

Regular seasonal migrations into the steppe, more so the tundra, are a new phenomenon in the biology of elk, at least over the last century. This ecological feature was acquired as a result of colonization. In the range a special region has been delineated, a region of summer habitation. This phenomenon is all the more significant since elk are essentially animals which lead a settled way of life.

241 Since 1950, notably from 1955 to 1958, the number of elk associated with tundra, especially those remaining in it for wintering, has steadily increased. Evidently, a special population of elk has been formed right before our eyes in recent years, not only in the steppes (see below) but also in the tundra zone.

Since 1951 the zone of distribution of elk to the south has also continued to enlarge. The southern boundary of the zone of permanent habitation has advanced and the region of visitation notably extended. This situation is explained by the fact that on leaving the zone of forest-steppes and steppes elk find only small sections convenient for permanent habitation. These are isolated, fairly large or sometimes even very small islands of forests. Visitations, however, extend even into the open steppes, sections of bottomland deciduous forests along rivers, small clearances, etc., i.e., into places where the animal cannot find satisfactory conditions for permanent habitation.

It is also significant that, having colonized the steppes, elk have now penetrated into densely populated and wholly cultivated open expanses where they find no shelter whatsoever. This is due not only to the animal's relationship to man ("anthropophilous"), but also to wintering conditions. Thus in the Kur' district some elk spread far into the forestless eastern and southeastern parts in spring, summer, and autumn, raise their young there, and go back in winter into the northwestern part of the range where there are more forests (D. Starodubchenko).

Transgressions are mainly irregular and aimless dispersals. Some of the animals die and some wander, probably for a long time, until they chance on some relatively favorable place in the south or return north. Thus two distinct modes of existence of the animal have recently been identified in the southern zone of the range as a result of movement farther south: small individual islands of permanent habitation along isolated forest masses or sections, and extensive areas of transgression with temporary, often very brief, residence. In these southern islands there are very few stray animals. Sometimes a few stray elk or a few dozen of them are sighted in a given region (Rovensk—about 15, Poltava—about 15, Kiev—about 10, Chernikov—about 75, etc.; A.P. Korneev). In such regions all the intervening areas between individual islands are visited only occasionally. South of the peripheral points lies a zone in which elk are only visitors, but frequent ones; farther south lie some areas where elk penetrate very rarely.

---

[229] Elk are often confined to such narrow and sparse forest and shrub "islets" that they cannot even hide in them on being frightened by man. Instead they run into the tundra and stay there until the source of disturbance has left the "islet".

The southern limit and range boundary after 1955 and in 1958 were as follows.[230] In the far west the southern boundary covered sections of permanent habitation which have yet to be exactly defined. Evidently, commencing at the state boundary somewhere between Belovezh Forest and Brest it ran east, passing slightly north of Pinsk, or in the region of Pinsk, and left at the junction of the Styr with the Pripyat.

From the mouth of the Styr the boundary runs upward along the river into the Roven district to the Stepan region (southwest of Sarna).[231] From there it turns west through Klesov region of the
242 same district (east of Sarna), runs in the same direction to the Olev region of Zhitomir district (Olev on Uborta), and later turns steeply southward into the Emil'chin region (Emil'chin at the source of the Uborta). From there the boundary line again runs west through the Lugin region to Korosten' (right bank of the upper reaches of the Uzh, tributary of the Pripyat[232]), and from there to the Razvazhev region of the Kiev district (lower reaches of the Teterev). Later the boundary line swings southwest toward Kiev.

The western boundary of the region of transgressions in this part of the right bank of the Dnieper commences in the Kiverets region of the Volynsk district (Kiverets, northwest of Lutska), runs straight west through the Tsuman region of the same district, and later in the same direction into Gorodnits region of Zhitomir district (Gorodnits on Sluchi northwest of Novograd-Volynsk). From there it arced north-east through Barashev and Chernyakhov regions into Zhitomir. Later it ran west-northwest into the Makarov region of the Kiev district (east of Kiev) and southeast into the region of Rzhishchev.

---

[230] The following outline of the southern boundary of elk distribution has been compiled on the basis of data (lists of regions of habitation, sometimes maps, etc.) kindly furnished by I.I. Barabash-Nikiforov (Voronezh), A.P. Korneev (Kiev—mainly data of the Central Board of Hunting, the Ukraine), Starodubchenko (Inspectorate of Hunting, Kur'), Mikhailov (Inspectorate of Hunting, Saratov), A.V. Fedosov and I.I. Ekimtsev (Inspectorate of Hunting, Bryansk), Sukhikh (Inspectorate of Hunting, Belgorod), Gusev (Inspectorate of Hunting, Rostov-on-Don), Vorshev (Inspectorate of Hunting, Stalingrad), and information from Severin, 1958; Alekseenko, 1958; Kompanets, 1958; Voloshko, 1958; Dolbanosov, 1957; and other data.

[231] Only the administrative region as reported by the correspondents has been cited as habitation. As an explanation the geographic position in relation to the center of the region has been mentioned.

[232] In the Zhitomir district there were only about 20 settled elk in five regions (A.P. Korneev).

Two instances are known of extremely deep transgressions beyond this line—to the Gorodok region of the Khmel'ntsik district (about 50 km west-southwest of Proskurov) and into Solobkovets region of the same district (about 50 km southwest of Proskurov). These two interesting visitations in which elk almost reached the Dnestr show that the possibility is not excluded even now of the independent penetration of the animal into the Carpathian forest district where it lived at some time in the past.

On the left bank of the Dnieper elk are dispersed extensively in the south in a large number of regions as a transgressor as well as a permanent inhabitant. This is mainly so in northern regions but also in some isolated regions far south.[233]

The line limiting the southern territory in which there are sections of elk inhabitation traverses the Dnieper at Kiev, later runs into the Borispol region (southeast of Kiev) and southeast to Pereyaslav-Khmel'nits. From there it turns east to the Chernukhin region of Poltava district (slightly east of Pripyat; Alekseenko, 1958), later southeast in the region of Dikanlka (north of Poltava), and straight north to the Gadyach region. From there, evidently bypassing Suma on the north, the boundary arced north and later east, passing into the Kur' district in the region south of Sudzha (Sudzhan region) or at the latitude of Suma. From there it runs east to the region of Staryi (possibly also Novyi) Oskol, then to Voronezh and southeast of Voronezh into Khrenov pine forest (Khrenovoe, slightly east of Bobrov).

From Khrenovoe the boundary line runs east to the Khoper, descends along it to the south and, encompassing the Medveditsa basin, runs to Stalingrad. The southernmost point of elk habitation in the Stalingrad district is the Leshchev tree farm in the Lenin region 40 to 50 km from Stalingrad. The largest number of elk inhabited the central part of the district, i.e., Frolov and Ilovlin regions (between the Volga, Don, and the lower reaches of the Medveditsa). It is possible that the zone of permanent habitation of the animal also covered the far northern regions of Rostov district (Veshensk, Chertkov, and possibly others also). In any case this represents a place of "permanent encounters with elk" (A. Gusev).

---

[233] The boundary given below is based on these southern points although the picture is not very clear north of it. Elk settled mainly in the south on the left bank region of the Kiev district and only transgressed in much of Chernigov (apart from the far north and northeastern parts) from 1955 to 1958 (data of A.P. Korneev).

The region of visitations between the Dnieper and Volga to the south can be described as follows. From Rtishchev on the right bank of the Dnieper the boundary runs across the Dnieper in the Chernobaev region of the Cherkassk district (slightly west of Zolotonosha), and from there following the general course of the Dnieper, to the Petrikov region of the Dnepropetrovsk district and toward Dnepropetrovsk. In this district there is on record a particularly deep 243 transgression to the Novopokrov region on the right bank of the Dnieper northwest of Zaporozh'e (Voloshko, 1958).

From Dnepropetrovsk the boundary runs east to Petropavlovka (at the mouth of the Byk River in Samara; Dolbonosov, 1957), then northeast to the Kremen region of Lugansk district (Kremenaya at the junction of the Krasnoi with the northern Donets), and from there southeast to the Staryi-Lugansk region (northeast of Lugansk beyond the northern Donets). Then it passes into the Rostov district at the Kundryuchya River (tributary of the northern Donets at its junction with the Don northeast of the city of Shakhta) and farther to the east into the Morozov region (south of the city of Morozov). From there, crossing the Tsimlyansk reservoir, the boundary passes into the Stalingrad district where instances of elk sightings in the steppes south of Stalingrad have been reported. Probably the boundary runs toward the Volga somewhere in the region of Cherni Yar. On the Volga itself transgressions of elk are known as far as Vladimirovka and Chernyi Yar. Possibly the animals descend from there along the floodplains of the river.

In the region under consideration an extremely interesting encounter with elk occurred at the end of summer, and another in December, 1958, toward Sambek village located close to the coast of the Sea of Azov (Taganrog Gulf) between Taganrog and Chaltyr (eastern Taganrog, Neklinov region with its center at Pokrovskoe). Such instances provide convincing proof of the past habitation of elk through the steppes right up to the coast of the Sea of Azov and of contacts between southern Russian and Caucasian populations. Under conditions of light cultivation of the steppes, and in other natural situations (bottomland deciduous forests along the steppe rivers), it is natural that the animal had settled not only in that region which is visited even at present, but also throughout the whole area up to the southern seas. On the other hand current transgressions of elk toward Chernyi Yar serve as an additional proof in favor of the view that elk reached the Volga valley in the past and even the delta on the Caspian Sea.

Thus the southernmost points of elk visitations lie roughly at 49° N lat. (Solobkovets region), 48° N lat. (Novopokrovsk region and Chernyi Yar), and 47°15′ (Sambek; southernmost point in Europe and the Kazakhstan steppes).

In the expanse between the Volga and Ural mountains and Ural River the boundary of the region of fairly permanent habitation of elk coincides with the Volga and runs north along the river to the mouth of the Great Irgiz. From there, along this river, it turns east and northeast and, in its upper reaches (already within the Kuibyshev district), turned steeply southeast and, encompassing the Teplov region (north of Ural'sk), exited toward the Ural River. It is evident that along Ural valley elk are present quite regularly even below Ural'sk. Above it, they live permanently along the Ural valley throughout the Orenburg district.

In the above region elk often emerge south into the steppe zones of Saratov district (recently, for example, Bezymensk, Krasnokut, Ershov, Ozinsk, and Klintsov regions) and also Stalingrad region. The southernmost points of visitations are the Urda region in the West Kazakhstan district (Urda, southeast of Lake El'ton), the steppe between Furmanov on the Great Uzen', and Chapaev (Lbishchensk) on the Ural at 50° N lat. and 50° E long., steppe slightly northeast of this place, Chapaev on Ural, and near the Ural in Taipak region at 49°35′ N lat. (Antonovo; Sludskii, 1953).[234]

Thus only in the extreme northwest, north of 50° N lat., to the west of the Dnieper, does the boundary pass through the forest zone, where it was altered extensively. Throughout the rest of the range it lies in the zone of forest-steppe but mostly in the steppe zone; much of the region of permanent habitation lies in this zone. Finally, the zone of visitations not only adjoined the semidesert and desert zones but even covers a considerable part of them.

Almost throughout its extension (apart from the far western section), the southern boundary of the range advanced far into the south compared with the 1880 boundary. On the right bank of the
244 Dnieper by 1958 it had not yet reached the boundary of the seventeenth and eighteenth centuries, but east of the Dnieper it penetrated

---

[234] In some of the above places elk were reported somewhat before the year 1955 to 1958.

deeper southward not only as a zone of transgressions, but partly (right bank of the Volga) also as a zone of permanent habitation. At some places the boundary of visitations has already approached, or even reached, the maximum possible reconstructed boundary.

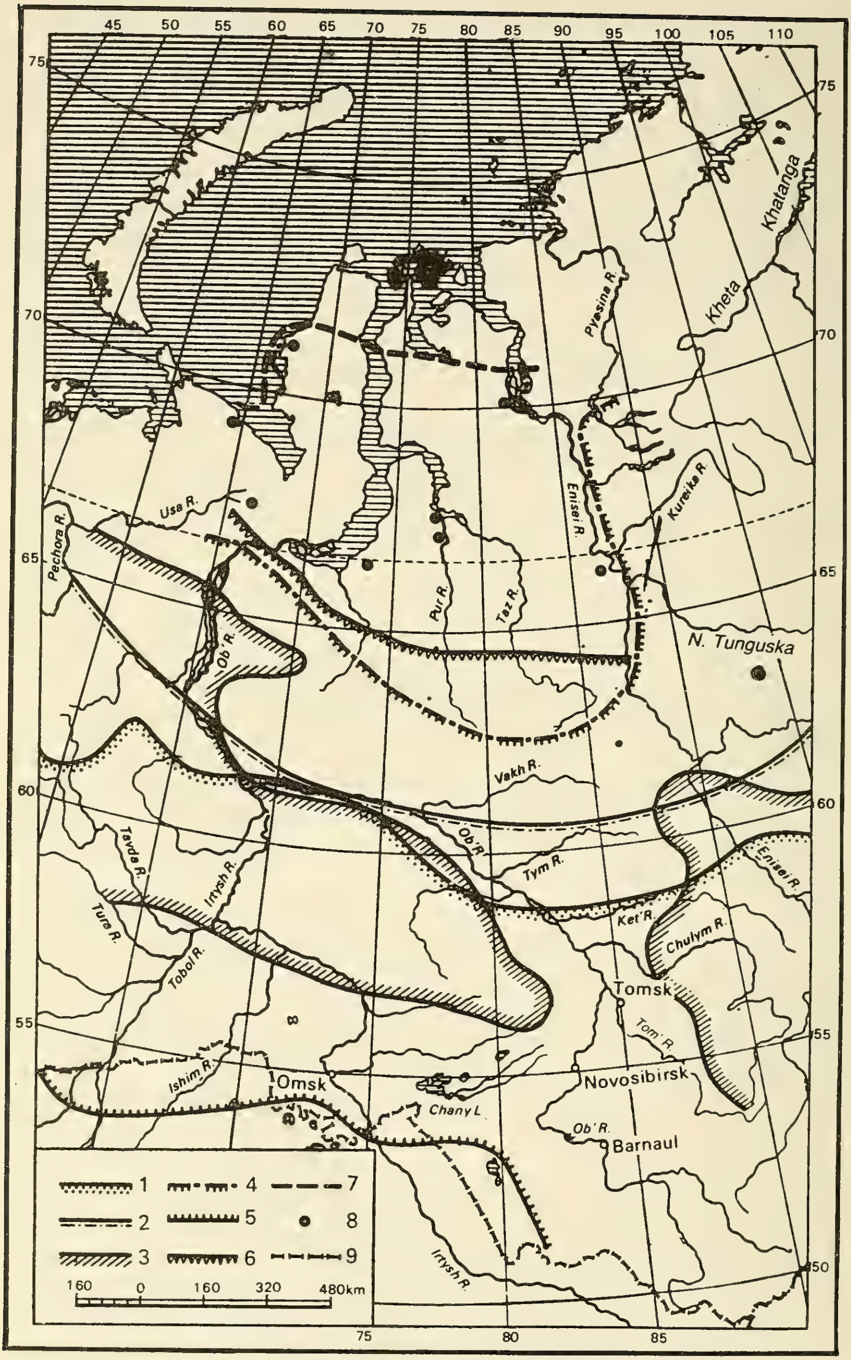
The recent (1930's to 1950's) map of elk colonization in the north, and especially in the south, represents a phenomenon of great importance, one influencing prevailing views about the ecological and geographic aspects of the species. This phenomenon is also of general biological interest (see below, colonization in Kazakhstan and western Siberia).

Geographic Range in Western Siberia and Kazakhstan

Reconstruction of the maximum range in this region over the historic period is possible only in a very general and partly tentative form because of the extremely scanty information available. In the north elk probably reached the forest boundary and the zone of its permanent habitation probably corresponded or was close to the present zone (Fig. 75). In the south it occupied the entire forest-steppe and the northern edge of the steppe zone. Between roughly 66 to 67° and 71 to 72° E long., the range boundary formed a prominent projection southward, reaching the meridional course (upper) of the Ishim (up to 51°30′ to 52° N lat.). In the east, roughly from Pavlodar to the latitude of Lake Markakol', the boundary ran along the Irtysh, then turned east, and ran toward the state boundary (E.I. Strautman, 1953; map). The range covered all of the Altai up to the boundary with Mongolia and Pri-Altai steppes. Farther away the range crossed beyond the Yenisey.

As in the case of the European part of the USSR, very significant positive and negative fluctuations of northern and southern boundaries of the range also took place in the territory under description. Information about these fluctuations, except for the Recent period, is far less than that available for the European part of the USSR, and pertains almost exclusively to the nineteenth century.

These movements, at least in the present century, have been occurring synchronously or fairly synchronously with westward movements. In any case, in the last decade the range of elk in western Siberia has enlarged notably both in the south and in the north. With respect to time and intensity, this enlargement has completely coincided with that occurring in the European part of the USSR. The northward movement of the animal in western Siberia and to the north and northeast in the European part of the USSR in particular represents a single process. Evidently the range contraction in


45
50
55
60
65
70
75
80
85
90
95
100
105
110
75
70
65
60
55
50
75
80
85
Khatanga
Kheta
Pyasina R.
Usa R.
Pechora R.
Enisei R.
Kureika R.
Pur R.
Taz R.
N. Tunguska
Ob' R.
Vakh R.
Tavda R.
Irtysh R.
Tura R.
Tym R.
Ob' R.
Enisei R.
Ket' R.
Chulym R.
Tobol R.
Tomsk
Tom' R.
Ishim R.
Omsk
Novosibirsk
Chany L.
Ob' R.
Barnaul
Irtysh R.
1
2
3
4
5
6
7
8
9
160
0
160
320
480km

Siberia in the nineteenth century described below also coincided in time with the corresponding phenomenon in the west.

Concomitant with enlargement of the region of permanent habitation, the number of visits beyond the limits of this zone has also increased greatly in the last decade. These transgressions have spread deeply in the north as well as in the south and elk have emerged not only into the forest-steppe, but also into the steppe, semidesert, and tundra zones.

In the nineteenth century (in the first half and middle) the range of elk in western Siberia shrank strongly. Its area decreased to a minimum, especially in the north. Compared to the maximum possible range (as at present) the northern boundary lay farther southward than in the west. Descending from the Urals, which it crossed around 60° N lat., the boundary crossed the Lozva roughly around 61° N lat. From there it formed a northward promentory running initially northeast roughly up to 62°, later turned southeast, and emerged toward the source of the Konda River. Later the boundary turned toward the Ob', somewhat below the mouth of the Irtysh, crossed the river, and ran for some time along its right bank not far from the valley. Slightly east of 75° it crossed to the left bank of the Ob', initially away from the river, later again coming close to it, and departed at the lower reaches of the Vasyugan. In the region of the mouth and lower reaches of the Ket' it again crossed to the right bank of the Ob'. From there, with a slightly southward arc, the boundary ran along the right bank of the Ket' into the Yenisey roughly at 59°30′ N lat. Beyond the Yenisey, though initially

---

245 Fig. 75. Boundaries of distribution of elk (*Alces alces* L.) in Trans-Urals and western Siberia (scale in km).

1—northern boundary during maximum contraction of range in nineteenth century (from Nasimovich, 1955); 2—rough outlines of northern boundary in 1920's and early 1930's (from Formozov, 1946); 3—boundaries of region of permanent habitation in 1920's and up to mid-1930's; between the two parts of the range and quite far in the north and south from the boundary line the animal appeared in those years as a visitor (from I.P. Laptev, 1958, with some modifications); 4—northern boundary of region of fairly permanent habitation in 1940's and by 1951 to 1952 (V.G. Heptner); 5—southern boundary in these same years; 6—northern boundary of region of permanent habitation at commencement and middle of 1950's (1955; I.P. Laptev); 7—northern boundary of visitations to tundra (from I.P. Laptev, 1958, with some additions); 8—some points of deep transgressions in the north; 9—boundaries in Kazakhstan (see Fig. 76 for southern boundary and transgressions southward).

Note: Second boundary at the Ob', Ural, and Pechora appears drawn extremely deep into the north; in those years elk did not cross 65° N lat. and probably lived considerably more southward (62 to 63° N lat.). V.G. Heptner.

246 slightly ascending northward (but not reaching 60° N lat.), the boundary line inclined south slightly and passed eastward (Nasimovich, 1955; map).

The southern boundary of the range at that time is not clear. However, judging from all the information available it lay quite far to the north and only very slightly more southward than the boundary shown below for the 1920's.

In the latter half of the nineteenth century the range evidently enlarged slightly. It was obviously large at the commencement of the twentieth century. However, by the early 1920's it was in a state of extreme contraction. The reasons for this are not fully understood but there is no doubt that some of the important contributory factors were immoderate hunting and killing of elk.

In its general outlines the northern boundary of the fairly permanent habitation of elk in the 1920's and early 1930's represented a deep southward arc. It commenced at the Pechora somewhere around 65° N lat., intersected the Ob' around 63° N lat., emerged along its right bank toward the mouth or the lower course of the Vakh, and then passed eastward to the Yenisey, running slightly north of the uppermost course of Tym. At the Yenisey the boundary departed roughly around 61° N lat. and turned eastward, rising slightly north and emerging at the midreaches of the Podkamennaya Tunguska (Formozov, 1946).

The above line reflects the northern boundary of only the zone of permanent habitation and that, too, schematically. The actual map of elk distribution in the 1920's and the first half of the 1930's is fairly complex. The range (zone of permanent habitation) is divided into two parts—western and eastern. The former was associated with the European part of the range and formed one single unit with it. Its northern boundary commenced at the Pechora somewhere in the region of the mouth of the Usa and proceeded toward the Ob', which was intersected at around 65° 30'. From there it turned southeast into the region of the source of the Kheta (left hand tributary of the Nadym) at roughly 64° N lat. and 71° E long. and later turned steeply west toward the Ob', encompassing the Kazym basin, and did not go within 80 km of the Ob'. Thus an eastward projection formed.[235]

---

[235] The range and boundaries described here and later are based on data of I.P. Laptev (1958) for the period 1920 to 1935. There is, however, every reason to assume that in the 1920's elk did not spread that far north along the Pechora and Ob'. At that time there was also no separately isolated section of permanent habitation of elk at the mouth of the Ob', as pointed out by the author (this section has not been marked). Along the Ob'

Farther away the boundary line turned straight south, leaving the Ob' roughly at 61 to 62° N lat., and descended along the Ob' up to the mouth of the Irtysh. Again intersecting the Ob' it ran along its left bank roughly up to the latitude of the mouth of the Tym and then gradually moved farther away from the Ob'. It intersected the lower reaches of the Vasyugan and ran southeast and south toward the source of the Om', initially in a slightly concave and later convex line. Having formed in this part of the Ob'-Irtysh interfluve region a large projection southeast, the range boundary became the southern boundary and turned west, initially through the upper reaches and later through the mouth of the Tara. Crossing the Irtysh there it later intersected the lowermost reaches of the Ishim and the lower reaches of the Tobol at the mouth of the Tavda, crossed the Tavda around 65° E long., and ran to the midreaches of the Tura.

The boundaries of the eastern part of the range in the north and west are as follows. The northern boundary commenced beyond the Yenisey, slightly north of 60°, and running west intersected the Yenisey just above the mouth of the Podkamennaya Tunguska. On the left bank of the Yenisey it described a gentle arc and turned northwest, reaching its farthest point around 61°20′ N lat. and 88° E long. The boundary turned south and ran sinuously in this general direction. It intersected 60° N lat. slightly east of the source of the
247 Tym, intersected the Ket' at roughly the same longitude, crossed Chulym around Zyransk, and departed toward the upper reaches of the Tom' in the middle interfluve region of the Chulym and Tom'.

In the expanse between these two regions of permanent habitation of elk lay a fairly broad region of 250 to 500 km where they were seen only as transgressors from one side or the other. Moreover, from both sides of the range elk moved considerable distances southward and very far northward (even up to tundra). Thus both zones of permanent habitation are linked by an extensive region in which elk transgressions are known. They were far from rare and a near-total exchange occurred between the two populations.

From the 1930's (more from the middle or end of that decade) the elk population began to increase and its range also to enlarge.

---

the boundary traversed evidently much more to the south, probably up to 63° N lat. It is evident that the line described (and the corresponding section in Laptev's map of 1958) pertained to the end of the period described by the author, i.e., 1935. In the 1930's the elk population had already begun to increase and the animal commenced to colonize, initially along the Urals and Ob'. The rest of the data of I.P. Laptev (1958) on range boundaries could be for the 1920's, i.e., the epoch of maximum contraction of the range in the present century.

Initially poor, the population became extremely large in the 1940's, peaking in the 1950's. The two sections of the range, formerly separated, joined to form a continuous range and its boundaries began advancing south as well as north. At the very end of the 1940's and by 1950 to 1951 the northern boundary of the region of fairly permanent habitation advanced north to a distance of 300 to 400 km and perhaps even more at some places.

By 1950 to 1951 a definitive arcuate line had formed, which commenced at the Ob' in the arctic circle at Salekhard (Obdorsk). From there it descended southeast quite steeply and intersected the upper reaches of the Nadym slightly north of 64° N lat. Running in the former direction, it proceeded farther toward the source of the Pur and, turning straight east, to the source of Taz. Turning northeast the boundary then ran toward the Yenisey evidently somewhere in the district of Zyryanov (between 63 and 64° N lat.) and turned straight north along the Yenisey. It evidently proceeded along the right bank slightly away from the river. In the lower reaches of the Yenisey, at the latitude of Dudinka, it departed to the east (V.G. Heptner).

Toward the mid-1950's (1955) the northern boundary shifted even farther. Intersecting the Ob' slightly below Salekhard, it ran southeast, intersecting 75° E long. not far from the coast of Tazov Bay and Nadym at 65° N lat. Then, taking an almost eastern direction and only slightly inclining southward, the boundary intersected the Pur roughly at 64°40′ N lat. and the Taz at 64°30′. It went off at 64°15′ N lat. toward Yenisey (I.P. Laptev. 1958).

On the whole, compared with the period of maximum range contraction in the nineteenth century, the northern boundary had advanced by a distance of 400 to 600 km or more by the mid-1950's. The northward advancement of the northern boundary continued during the latter half of the 1950's.

In exactly the same manner as in the European part of the USSR elk penetrated far north beyond the above-described line into the forest-tundra and open tundra devoid of any forest vegetation. In this vast expanse (extending up to the sea coast) lying north of the boundary line visitations extended for a greater distance than in the west. They became more frequent and were on a larger scale in the 1940's and more so in the 1950's. At some places the summer movement of elk to tundra was a fairly regular phenomenon although it had not yet assumed the form seen in Bol'shezemel' and Malozemel' tundras in the west.

On the whole the northern boundary of the zone of elk transgression lay in the Yamal and Gydan peninsulas, roughly at 71°00′ to 71°30′ (I.P. Laptev, 1958).

The significant curvature of the northern boundary of elk, so sharply manifest in western Siberia and also in the Pechora basin, partly also in Trans-Yenisey Siberia, attracted attention in the 1920's and 1930's and even earlier (recent references include Yurgenson, 1935; Podarevskii, 1936; Formozov, 1946; Nasimovich, 1955; I.P. Laptev, 1958). At one time the view prevailed (Podarevskii, 1936; Formozov, 1946) that the absence of elk in the region of this curve was due to snow height there. In the Pechora basin, northwestern 248 Siberia (Nadym, Pur, and Taz basins), and the basin of the lower Yenisey, the snow cover is maximum for the elk range as a whole (not less than 90 cm or so).

The northern colonization of elk in the region of maximum snow described above proves that the snow cover should not be adduced as an explanation for the curve in the boundary. Hunting of the animal was of vital importance and deep snow only facilitated its extinction (Nasimovich, 1955).[236] That elk have not as yet permanently colonized the forest zones in the basins of Nadym, Pur, and Taz, and along the left bank of the lower course of the Yenisey can only be a temporary phenomenon. If the dispersal process had not been artificially interrupted (by extinction), elk would still have continued to colonize these areas in the same manner as they did in the corresponding territories beyond the Yenisey (see below). At the same time it is possible, as sometimes assumed (I.P. Laptev, 1958), that the penetration of the animal there was impeded or rendered difficult by the absence or inadequacy of some important food sources.

The beginning of elk colonization in the south and the advancement of its southern boundary corresponded in time to the northward movement described earlier. It commenced evidently at the end of the 1920's and advanced perceptibly in the 1930's when the first of the visitations, sometimes over long distances, were noticed in the southern margin of the forest zone, the forest-steppe of western Siberia, and some individual places even in northern Kazakhstan. This phenomenon assumed vast proportions in the 1940's. By the end of this decade in the south of western Siberia the elk had become a permanent inhabitant not only of the southern edges of the forest zone, but also of considerable parts of the forest-steppe. In the 1940's elk visited the steppes of western Siberia and the northern and eastern periphery of Kazakhstan fairly extensively and became permanent inhabitants at some places.

---

[236] If not subjected to thoughtless persecution, and food sources are adequate, elk can survive in areas with a snow thickness of over one meter.

In the 1950's this process continued and elk colonized the steppe zone, although this period was evidently characterized not so much by an enlargement of the range, as by an increase in population and colonization of the animal at places where it was seen only as a transgressor in the previous decade. The natural limit of southward distribution attained its general features in the 1940's.

The southern boundary of the region of permanent habitation of elk in western Siberia and Kazakhstan at the commencement of the 1950's (by 1952) occupied the following position. Commencing in the west at Ural'sk, it proceeded along the Ural valley eastward to Orsk. From there, in a manner not precisely known, it rose north along the interfluve region of the upper Ural and the source of the Tobol roughly up to the latitude of Troitsk. Evidently, bypassing Troitsk to the north, or going through it, it turned steeply east toward the Tobol through the northern Kustanai district. Including the Vveden region (Vvedenka) within the range, the boundary turned sharply south toward the region south of Kustanai, and then encompassing islands of cut-over forests at Ara-Karagay to the east and southeast of Kustanai, turned east toward the Ishim through the region of Lake Ubogan.[237] There the boundary, running in the same direction, traversed along the latitude 53°30′ (at places probably even slightly more southward), including in the range all, or nearly all, of northern Kazakhstan in the east roughly up to 71° E long. From there the boundary inclined northward slightly and, passing north of Lake Seletytengiz, crossed the Irtysh around 52°30′ to 53°00′ N lat. From the Irtysh it proceeded in the form of a gentle, slightly northward arc toward Lake Kulundinsk, passed it on the east, and running slightly east of 80° E long. turned to the Altai.

It can be seen from the above brief description that by the early 1950's (by 1952) elk had colonized not only the whole of the forest zone and the entire forest-steppe, but also a considerable part of the steppe zone. The region of transgressions by that time was much
249 more extensive and the latter occurred so often at some places that a fairly permanent habitation or a tendency toward it may be

---

[237] Evidently, by that time elk already lived in Aman-Karagai pine forests roughly 100 km south of Kustanai (north of Seminozernoe). There is no first-hand information on this, however.

assumed.[238] In western Kazakhstan, along the Ural, elk intruded south up to 49°35′ (Taipak region, West-Kazakhstan district) and, along the steppes east of the Ural, into the region of Dzhambeita and adjoining places (roughly 50° N lat. or slightly more). South of the Ural, between the river and parallel to Aktyubinsk and Orsk in the east, elk appeared in the steppe at several places. More southward, they reached the source of the Orsk (observed in the south up to 49°15′ N lat.) even closer to the boundary of the semidesert. Farther to the east, after a fairly distinct break, frequent transgressions of elk have been recorded at several places to the north, west, and east of Kustanai. South of Kustanai elk intruded even as far as 52° N lat.[239]

In the Kokchetav district, the one lying south of the North-Kazakhstan [district], numerous instances of transgression have been recorded throughout almost all of the district to the east of 71° E long. It is possible that in the northwestern part of the district elk by then had begun to colonize or tended to do so. South of this part of the Kokchetav district instances of transgression were known in the northern part of Akmolinsk [district] to 52° N lat. and even slightly more to the south, to Atbasar, i.e., to the Ishim between 68 and 70° E long. No transgressions were reported in this period between 71 and 73° E long. Elk occurred between 74° E long. and the Irtysh only in the far north of Kazakhstan; farther south a transgression was reported at 74° E long., roughly as far as 52°30′ N lat.

Along the right bank of the Irtysh elk normally lived in the region of Lake Chany and south of it, and along the Pri-Altai steppes with their ribbons of pine forests. Transgressions from there in the direction of the Irtysh and to the Irtysh itself were known at several places throughout the stretch of the river to the south almost up to Usk-Kamenogorsk.[240] In the very south they probably came from the Altai.

---

[238] Evidently the situation along the Ural valley below Ural'sk (Chapaev and Taipak regions).

[239] From the region of Kustanai and Ubogan and from Ara-Karagai forest at Kustanai, which elk had already colonized, to this place for not less than 150 km, about 100 km is an open steppe with only tiny lakes up to Aman-Karagai pine forest (at Semiozernoe) and the rest again steppe. Two transgressions have been recorded there, one in 1939 and another in 1940.

[240] The dispersal and dynamics of the elk range in western Siberia and Kazakhstan, in spite of innumerable articles and minor notes referenced in the text, are based on data compiled by Middendorff, 1851, 1867, 1869, and 1874; Yurgenson, 1935; Kulagin, 1932; Formozov, 1946; Yanushevich and Blagoveshchenskii, 1952; and others, but mainly based on the data and compilations of Sludskii, 1953 (Kazakhstan); Nasimovich, 1955; and I.P. Laptev, 1958.

Thus in the early 1950's elk were present in all the places in which they were known in the eighteenth century.

In some of these regions, reckoned above as places of transgression, the animal during this period was already resident and multiplying.

Unlike the European part of the USSR, no significant changes occurred after the 1950's in the disposition of the southern boundary of the general zone of elk distribution in the southern part of western Siberia and Kazakhstan. The animal evidently reached the natural limit even before this period. In any case, in 1958, apart from some particularly deep transgressions, elk were generally encountered within the boundaries of 1952. Possibly some expansion of the region of transgressions took place west of Tobol (western Kustanai), but on the other hand there was some retreat to the west of the district boundary, north of the upper reaches of the Ishim (A.A. Sludskii).[241]

It is evident, however, that the population of the animal and its density increased in the southern zone of the range. As a result, there were some changes in the nature of residence of the animal in some individual places in the range under discussion: in places where elk were formerly transgressors they began living permanently or almost so, and in places where transgressions were rare, the same
251 became more regular, the boundary of permanent habitation had slightly advanced southward by 1958 but positive data about this phenomenon are not available.

The increase in elk population along the southern margin of the range is also borne out by deeper, farther southward transgressions in the 1950's. In recent years, before 1958 and in that year, elk intruded into the region southwest of the source of the Ilek (in Tamir region), the region between Chelkar settlement on the railway line and Mt. Irgiz, the Dzhetygarin region of Kustanai district (north of the source of the Tobol), the Ulutau mountains, the region between Lake Tengiz and the Ishim, the mountains in the region of Bayansk-Aul, and the mountains in the region of Karkaralinsk (A.A. Sludskii). These points lie in the zone of steppes, at Temir in the semidesert, and at Chelkar even in the desert zone.

In all the maps on elk colonization in the steppes (in Kazakhstan) certain areas stand out prominently. In the west movement proceeded from one side along the Ural valley, and from another side, also in relation to the Ural valley, from the Orsk region in

---

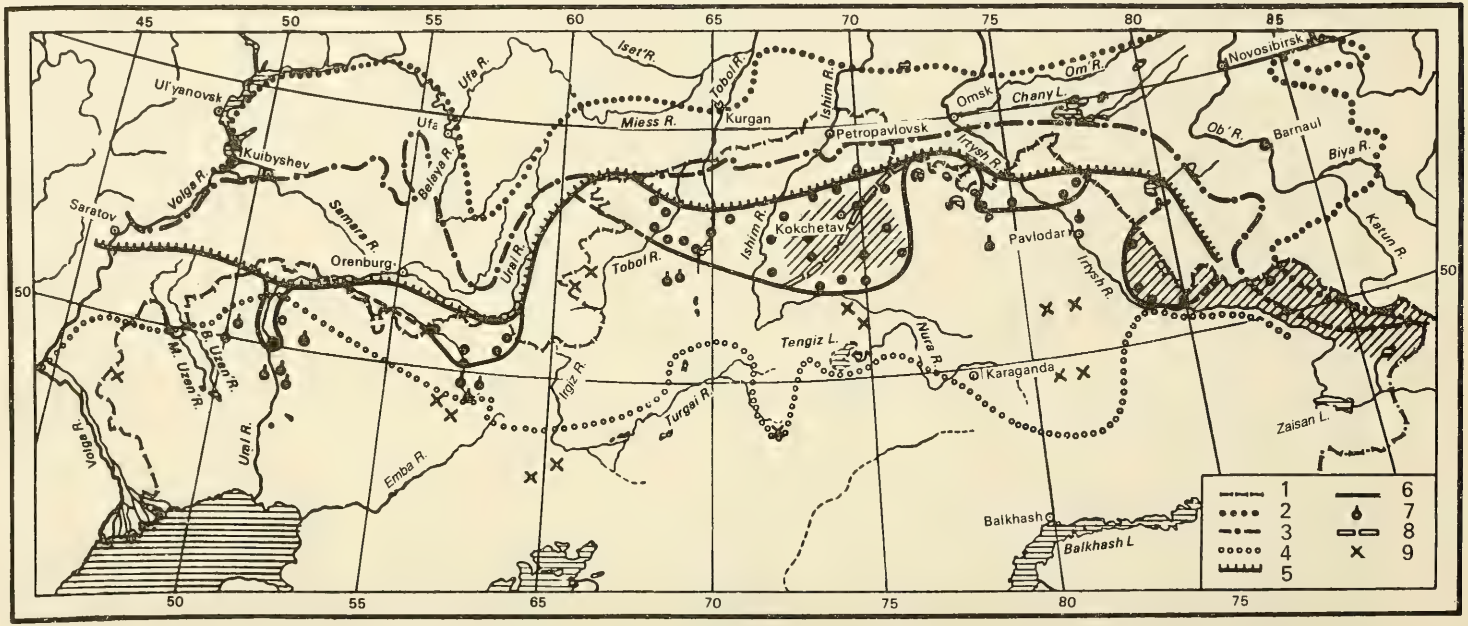
[241] This is probably associated with the natural changes occurring in the northern parts of Kazakhstan in recent years and represents a special local phenomenon.

Aktyubinsk. In the central part of Kazakhstan the broad front of colonizing animals moved into the area from the zone adjoining the Tobol in the west up to roughly 71° in the east. In almost all cases migration was associated with river valleys, trees and shrubs in bottomland deciduous forests, clearances in steppes and forest sections, and pine groves in steppes and in small elevations, and rarely along rushes by lakes. This part of Kazakhstan is particularly favorable in this purely biotopic context. Sometimes the animals moved south and into open steppe and, more interesting, even penetrated the semidesert and true deserts.

It should be emphasized that this front, especially between 67° and 71° E lat., is moving in the direction of those places where elk in Kazakhstan existed in the eighteenth century, and thus the restoration of the former range proceeds very intensely. Furthermore although there are no direct references to it, elk formerly lived also in the forests north, west, and east of Kustanai and also in the pine forests of Aman-Karagai 100 km south of the town.

In western and central Kazakhstan advancement was from the north. In a third of the zone, along the Irtysh, colonization proceeded probably mainly from the east from the Pri-Altai steppes with their ribbons of pine forests and the Kulundin steppe and, to a lesser extent, from the north from the region of Lake Chany and Omsk.

Very little information is available about elk distribution in the Altai. In the period of peak range expansion in the historic period elk occupied, as shown before, the whole of this montane area up to the state boundary, apart from places like the Chuisk steppe which are unsuitable for survival. In the south the range evidently extended into the Narym range and probably also to the Kurchum; the boundary traversed Lake Marka-Kol' or slightly north of it. This was possibly the situation by the early nineteenth century. Subsequently elk range in the Altai shrank drastically. It continued to contract at the end of the last and at the commencement of this century when, generally speaking, this process ceased in western Siberia. By the 1930's elk had practically disappeared in much of the Altai and were preserved only in the easternmost and northeastern parts by the middle of that decade. There elk occupied the Chulyshman basin and part of the basin of the Bashkaus (a tributary of the Chulyshman) and the region of the upper courses of Bol'shoi and Malyi Abakan and the source of the Lebed'. Slightly to the west they occurred in the zone adjoining Lake Telets from the west and in the source of the right-hand tributary of the Katun, i.e., Kodrin (Dmitriev, 1938; V.G. Heptner).


45
50
55
60
65
70
75
80
85
Novosibirsk
Om'R.
Chany L.
Omsk
Ob'R.
Barnaul
Biya R.
Katun R.
Iset'R.
Tobol R.
Kurgan
Ishim R.
Miess R.
Petropavlovsk
Irtysh R.
Ul'yanovsk
Ufa R.
Ufa
Belaya R.
Kuibyshev
Volga R.
Saratov
Samara R.
Orenburg
Ural R.
Tobol R.
Ishim R.
Kokchetav
Pavlodar
Irtysh R.
50
50
B. Uzen'R.
M. Uzen'R.
Tengiz L.
Nura R.
Karaganda
Irgiz R.
Turgai R.
Zaisan L.
Volga R.
Ural R.
Emba R.
Balkhash
Balkhash L
1
2
3
4
5
6
7
8
9
50
55
65
70
75
80
75

The boundary outlined above may be regarded as corresponding to the state of utmost reduction of the range. Later, but before the recent period, although it enlarged there is almost no positive supporting information. Range expansion and population increase evidently occurred not only in the eastern section described above, but also with the arrival of animals from the north and their colonization of the foothills. Instances are known, for example, of the appearance of elk around Biisk (Kuchin, 1958). It is possible that elk transgressions in the upper Irtysh (toward Ust-Kamenogorsk—see above) were associated with their increasing population and range expansion in the Altai.

252 *Geographic Range in Trans-Yenisey, Siberia, and the Far East*

Reconstruction of the elk range east of Yenisey in the period of its maximum development in the historic period is extremely difficult because of scanty information. Data are available to show that in the Taimyr, elk reached 71 to 72° N lat. (Middendorff, 1869), approached very close to the Kolyma estuary (Filippovka River; Wrangel, 1841), and were widely dispersed in extreme northeastern Siberia. In general, however, with the exception of some places, the boundaries of the maximum range in the past could be regarded as closely corresponding to those that existed in the middle and latter half of the 1950's.

As in western Siberia during the same period (commencement and middle of the last century), a contraction of the range took place in central Siberia also. This process evidently did not cover the eastern part, i.e., the Lena basin and farther east. Boundary fluctuations did take place there, for example in the Kolyma, but they were

---

250 Fig. 76. Boundaries of distribution of elk (*Alces alces* L.) in the Trans-Volga, south of western Siberia and in Kazakhstan (scale in km).

1—boundary of Kazakhstan; 2—southern boundary of forest zone (taiga); 3—northern boundary of steppe zone (between lines 2 and 3—forest steppe); 4—northern boundary of semi-desert and desert zone (between lines 3 and 4—steppe zone); 5—southern boundary of zone of permanent habitation of elk in the early 1950's (by 1950; based on data of Sludskii, 1953 and I.P. Laptev, 1958, with some modifications and additions); 6—southern boundary of region of elk transgressions in the 1930's and 1940's and early 1950's (by 1952), and some points of transgressions within it; 7—some especially distant transgressions of elk before 1952; 8—boundary of zone of elk distribution in 1958; 9—especially deep transgressions of elk at the end of 1958 (nos. 8 and 9 from A.A. Sludskii); 10—zone of elk habitation in Kazakhstan in the past. Boundaries of natural zones schematic. V.G. Heptner.

evidently exceptions and their magnitude small.

During the period of extreme recession the northern boundary of the range commenced at the Yenisey roughly at 59°30′ N lat. and turning east ran to the uppermost course of the Podkamennaya Tunguska. In this expanse the boundary formed a gentle arc slightly curved northward. However, it did not run along the above river and did not reach 60° N lat. From that place on the Podkamennaya Tunguska the boundary line made a steep loop and encompassed from the south the interfluve region of the sources of the Podkamennaya and Nizhnyaya Tunguska, turned north along the upper reaches of the Nizhnyaya Tunguska (slightly east of it), and crossed the river in the region of 63° N lat. From there, slightly inclining west, it ran to the upper reaches of the Kotuya (Nasimovich, 1955). Farther away in the east the northern boundary even at that time lay far in the north, probably along the forest boundary.

In the present period (middle and latter half of the 1950's) the northern boundary in this territory commenced at Lake Pyasino (east of Dudinka on Yenisey; V.N. Skalon). In a manner not clearly understood, but probably along the northern boundary of forest-tundra, i.e., along 71 to 72° N lat., it proceeded evidently to the mouth of the Khatanga or the lowermost reaches of this river and later into the lower reaches of the Anabar. It intersected the Anabar at 72° N lat. (slightly south of Syskylakh) and ran in the form of a slightly irregular line to Olenek around 71°30′ N lat. From there it proceeded to the Lena, running toward it at Kyusyur or slightly north of it (about 71° N lat.).[242]

East of the Lena, corresponding to the shrinkage of the range in the tundra, the boundary ran southeast, proceeding on 70° N lat., and later again rose northeast to the Omoloi slightly south of 71° N lat. From there it ran to the Yana, intersecting it at Kazachego or slightly north of it (71° N lat.). On the Khorma the boundary went only slightly southward, but formed a slightly southward bend between 138 and 144° E long., not reaching 70° N lat. On the Indigirka the range boundary went slightly south of the Chokurdakh, intersecting the river roughly at 70°30′ N lat. From there the boundary ran southward. It intersected 150° E long. at 70° N lat., Alazeya at 69°30′, Chukoch'ya around 69° N lat. and the Kolyma at Nizhni Kolymsk or slightly farther north (around 68°30′). At this latitude, descending slightly farther, it ran into the basin of Bol'shoi and Malyi Anyuya beyond Yakutia.

---

[242] It is possible that along the Lena, as also along some other rivers in Europe and Asia, elk extended far into the north. Instances of transgressions are known even in 1928 to Cape Bekov in the Lena delta at 72°30′ N lat. (Kolyushev, 1936).

This boundary in Yakutia (i.e., between the Anabar and Kolyma) traversed along the southern boundary of the tundra, partly through forest-tundra. As a result of the general increase in numbers, commencing from 1954, fairly regular seasonal (summer) dispersal of elk into tundra was observed, especially east of the Yana, the animals reaching several places along the sea coast. The dispersal evidently occurred mainly along rivers but also in open tundra. Thus, between 140 and 142° E long. elk emerged up to 72°. In the region of the lower reaches of the Khorma up to its mouth (72°), along the Indigirka up to its delta (almost 72°), along the Alazeya, and in 253 tundras adjoining it from the east, the animals reached the sea around 71° N lat.[243]

The range is known poorly to the east of the Kolyma in far northeastern Siberia. In this region, essentially devoid, or almost devoid, of forests, conditions for survival of elk are hardly favorable. The animal is forced to confine itself to river valleys, mainly in willow thickets, and at places poplar groves. As a result, not only is its population very low but also the boundary itself bears a complex outline and is extremely unstable. It is very difficult to demarcate the region of fairly permanent habitation from that of transgressions of individual animals. Moreover, the available information pertains to very early periods, i.e., the 1920's and 1930's.

From the above place in Kolyma the boundary ran east, encompassing Malyi and Bol'shoi Anyuya basins, and later turned south, covering the upper reaches of the Anadyr or at least the region of the left hand tributaries of the upper Anadyr—the Yablon and Yeropol. It is possible that elk dispersed (transgressions?) downward along the river roughly to Markovo. From there the boundary ran south into the source of Penzhina and, leaving the Taiganos Peninsula outside the range, ran toward the Okhotsk coast in the northern part of Gizhigin Bay. Formerly elk normally reached Markovo along the bottomland deciduous forests of the Anadyr and, in the remote period, evidently even up to the lower reaches of the Anadyr or even the sea coast (Kanchalan River, flowing into the Anadyr estuary, Amerikanskaya Koshka).[244]

In the distant past (seventeenth and eighteenth centuries) elk were distributed more widely and probably were encountered along the bottomland deciduous forests and other rivers of the northeastern extremity of Siberia. Instances are known of elk remains from the ocean shore at Cape Schmidt (Nordenskiöld, 1870; cited by Nasimovich, 1955). Deep transgressions are known even more recently, for example in 1936, on the Bol'shoi Baranikh River around 69°30′ N lat. and 166°20′ E long. at a distance of 120 to 150 km north of the forest region (Portenko, 1941). It is possible that in the past and possibly in the recent period, from the upper reaches of the Penzhina the boundary ran along the river to the coast of Penzhina Bay, or Penzhina was frequented by wanderers.

---

[243] Range boundary in Yakutia is based on unpublished data of D. Ivanov (Yakutia).

[244] According to data published by Portenko, 1941. According to Abramov, 1954 (map), the boundary ran along the midportion of the Bol'shoi Anyuya, upper course of the Malyi Anyuya, and through the sources of the Yablon, Yeropol, and Penzhina.

From Gizhigin Bay the boundary ran along the sea coast southward to the Ussuri region; elk were absent in Kamchatka, the Shantar Islands, and Sakhalin.[245] Along the coast of the Ussuri region the boundary ran south roughly up to the mouth of the Amgu River (around 46° N lat.). From there it withdrew from the coast into the mountains and extended in the form of a narrow projection along the more elevated parts of Sikhote-Alin up to the source of the Iman (around 44°45′ N lat.; Kaplanov, 1948). In the middle of the last century, and also much later, it extended along Sikhote-Alin up to the upper courses of Ussuri and Suifun, i.e., up to 43°30′ N lat. (Przewalski, 1870). In the region of the mouth of the Imansk the range boundary intersected the Ussuri, exiting in the west into China.

In the expanse from the Ussuri to the Altai the elk range currently crosses through the southern boundary of the state or runs along it, as for example in the Tannu-Ola range. The range boundary deviates from the state boundary somewhat significantly only in the eastern and western Trans-Baikal steppes, which it encircles from the north.

This is evidently the situation also in some other places, but the curvature of the boundary line to the north is less significant and hardly associated with topographic features (extremely high mountains for example). On the whole the southern boundary of elk is known only very generally.[246]

Geographic Range outside the Soviet Union

At present[247] the American range of elk is considerably reduced although it preserves in general the outlines of a zonal range, 254 extending from Alaska to Nova Scotia. Unlike the range of American wapiti, of which only three prominent and some tiny sections have remained, it is not only still very extensive but also forms a single block (Burt, 1952; Seton, 1909–1910). As in the USSR, in America also elk became better adapted than deer to living in the proximity of man. Some periods are known in recent times during which elk advanced slightly into the south and at places into the north. However, there has been no significant increase in range, at least not to the extent seen in the Soviet Union.

---

[245] According to Abramov (1954) the boundary ran toward the Okhotsk coast only in the region of Tauisk Bay; it extended northward away from the sea along the divide of the Kolyma range.

[246] See the section on western Siberia for elk distribution in the Altai.

[247] See the description of the genus for the reconstructed range.

In Europe, in much of its natural range, i.e., in western and central Europe, elk became extinct even around the tenth century. Up to the eighteenth and nineteenth centuries elk survived only in the far eastern parts (not including the USSR)—in Saxony until 1746, Galicia until 1760, Silesia until 1776, and Polish Pri-Baltics until 1830. In Rumania (Carpathians) elk evidently died out in the eighteenth century. In the twentieth century and before the Second World War some (at places considerable) elk were present in eastern Poland. At present in the German Democratic Republic and Federal Republic of Germany elk are altogether absent and present in Poland only in the northern and northeastern parts. They are common in Finland, Sweden, and Norway. On the Scandinavian Peninsula the elk population has increased significantly and the animals have advanced extensively into the south in recent years and wholly colonized the peninsula up to its southern extremity.[248]

In Asia, outside the USSR, elk live in Mongolia and northeast China. In Mongolia they occur in the Hobsogol region in the east and in the west up to the State boundary of the USSR, along the left bank of the Egin-Gol and Selenga in the east up to 105° and in the north up to the frontiers and Hentei. Here elk live in the south to Bogdo-Ula (slightly southeast of Ulan-Bator) and in the west to the Tola, almost up to its confluence with the Orhon. The Khentei section of the range joins with the Soviet section in the expanse between 108 and 111° E long. and forms a projection of the Siberian range southwest (Bannikov, 1954).

In northeast China elk live along the northern part of the Great Khingan, slightly penetrating even into the easternmost corner of Mongolia at Il'Khuri-Alin and the Little Khingan. Evidently elk also inhabit the northern parts of the eastern Manchurian montane region, but information regarding this is inadequate. (V.H.)

---

[248] In recent years instances are known of the appearance of elk on Zealand Island in Denmark. The animals swam through Sund Strait, which is about 10 km wide at its narrowest point.

Geographic Variation

Geographic variation in elk has been well studied and the literature is quite substantial. Yet views on the number of species and geographic races vary considerably. For the entire range of the species, including America, two species with seven subspecies have been proposed (Flerov, 1931 and 1934). Of these, both species and three of the seven subspecies occur in the Soviet Union. According to another view (Buturlin, 1934) a single species of elk is acknowledged for both the Old and New World and four subspecies for the Old World and the USSR. Finally, it was recently suggested (Flerov, 1952) that there is only one species of elk with a single form for Europe and western Siberia, one for the Caucasus, and one for all of the Trans-Yenisey part of the range and the whole of the American range.

Elk are fairly mobile and a considerable population mixing, especially in certain periods, has occurred, hindering the emergence of intraspecific geographic differentiation. Nevertheless, it does exist and there is no doubt that the recent view about the existence of only two forms of elk (not counting the Caucasian) is erroneous. In the Old World and the USSR there are four fairly well defined forms, possibly even six (see below). In the New World there are evidently only two subspecies. The subject calls for further study with adequate material. The following forms are present in the USSR.

255 1. European elk, *A. a. alces* Linnaeus, 1758 (syn. *coronatus, europaeus, machlis, antiquorum, palmatus, jubata, typicus, uralensis, meridionalis*, and *tymensis*). Medium to fairly large animals but not the largest. Body length of bulls up to 270 cm, height at withers up to 216 cm, and weight up to 500 kg or more (in exceptional cases up to 620 kg). Total length of skull of bulls 550 to 580 mm and length of rostral part (from anterior edge of orbit to tip of premaxillae) 329 to 347 mm. Antlers with fairly well developed, sometimes well-developed palmate portions with a span of 135 cm; weight (without skull) up to 20 kg. Palatine processes of premaxillae in front of vomer narrow and form a groovelike depression; total width less than, or equal to, vertical diameter of infraorbital foramen. Nasal processes of premaxillae not constricted upward but enlarged like a spatula with a blunt terminus (Flerov, 1952). Color of animal described earlier (legs light-colored).

Found in the European part of the USSR, Urals, in the east roughly to the Yenisey, western Siberia, and Altai. Outside the USSR occurs in Europe.

This form is not completely homogeneous throughout its exten-

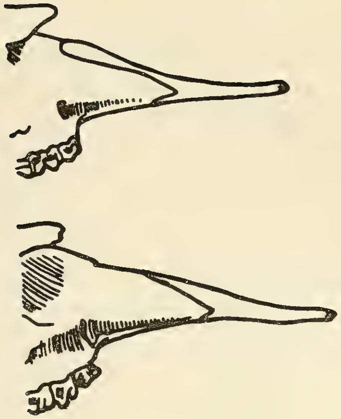


Fig. 77. Rostral portion of skull of elk (from Flerov, 1952).
Top—European and western Siberian (*Alces alces* L.); Bottom—Yakutian (*Alces alces pfizenmayeri* Zuk.).

sive range. Animals inhabiting western Siberia are significantly larger, heavier, and have more powerful antlers with a distinctly developed palmate portion. Those in the European part of the USSR, especially from the more western parts, have a body length of 250 to 270 cm, height at withers of 175 to 185 cm, and weigh up to 480 kg (usually 320 to 400 kg). Western Siberian animals attain the maximum of the above limits in size, weight, and antlers.

Before the Revolution differences were largely associated with the fact that in the European part, in view of excessive hunting, killing of the best males, and some other reasons, the range of these animals narrowed down and at places even disappeared totally (in the west). In western Siberia the population was preserved under normal conditions and the animals could attain full development. There is, however, no doubt that differences were also due to natural factors, the above conditions only accentuating them and rendering them sharper in the last decade before the Revolution. Under present optimal conditions for animals in the European part of the USSR elk are completely protected.

The taxonomic status of western Siberian forms requires a study based on new material from Siberia and Ural. The name *uralensis* Matschie or *tymensis* Zukowski may prove suitable for western Siberian elk.

2. Caucasian elk, *A. a. caucasicus* Verstschagin, 1955*. Small size.

---

*Spelling of author's name in taxonomic divisions is sometimes at variance with spelling in text and bibliography because the Israeli orthography has been used in this translation—General Editor.

Skull length 538 mm (one animal) and length of upper tooth row 136 to 138 mm. Skull similar to European type. Nasal processes of premaxillae enlarged at ends, sometimes reaching nasals. Facial part in rostral region more intensely contracted than in northern elk. Palmate portion of antlers very poorly developed. Coloration and body dimensions not known.

Found in forests of premontane plains in northern Caucasus, bottomland deciduous forests, and reed thickets on the Kuban and Terek. Evidently also occurred in the lower reaches of the Don and probably the Kolkhid lowlands. Extinct by early nineteenth century. Outside the USSR not known, but probably penetrated adjoining parts of Turkey by way of Batumi.

3. East Siberian or Yakutian elk, *A. a. pfizenmayeri* Zukowski, 1910 (syn. *yakutskensis, angusticephalus, ? bedfordiae;* the names *americanus* and *gigas* are used in Soviet literature for this form). 256 Larger than western elk. Body length up to 300 cm, even more in exceptional cases; height at shoulders 225 to 240 cm; weight 570 kg or even 620 to 655 kg. Skull length in males up to 585 to 620 mm and width of zygoma up to 240 mm.

Antlers very large and massive, usually with large and broad palmate section and large number of short tines, including large, stunted, and bifurcate anterior tines separated from palmate section. Antler span up to 159 cm, width of palmate section up to 60 cm, and circumference of rosette up to 42 cm; antler weight may considerably exceed 20 kg. Palatine processes of premaxillae in skull in front of vomer broad and flat and do not form a groovelike depression; their total width exceeds vertical diameter of infraorbital foramen. Nasal processes of premaxillae constricted and ends honed, wedgelike, and not enlarged like a spatula.

Coloration same as in European elk but with slightly greater admixture of gray tones in winter and slightly darker, sometimes altogether black limbs, almost indistinguishable in color from trunk (Flerov, 1952). Dewlap usually larger than in western forms.

Found in Siberia east of the Yenisey and in the Far East except the Amur and Ussuri region (i.e., in the south evidently to the Stanovoi range). Outside the USSR occurs in the northern periphery of Mongolia (Pri-Kosogol, Khangai, and Hentei).

Elk in this territory represent a special form, well distinguished not only in body size and some color characteristics (less specific) but also craniologically. These features (especially the craniological) draw the eastern Siberia elk rather close to the American moose which, from the viewpoint of zoogeography, is quite understandable and natural. In fact an attempt has recently been made (Flerov, 1952) to place all elk from the entire Trans-Yenisey Asiatic part of the USSR (including the Ussuri region) under the form *americanus* described from the northeast USA, grouping them with moose of North America, including Alaska. This viewpoint, insofar as the taxonomy of eastern Siberia elk is concerned, cannot be accepted.[249]

Throughout the extensive range of its distribution this form is not really identical. Northeast Siberia i.e., the Kolyma-Indigirka basin and forests of the Anadyr basin are colonized by particularly large-sized animals, the largest of all elk seen in the USSR (maximum among Russian elk), with extraordinarily large antlers. It has been suggested (Buturlin, 1934) that this form constitutes a distinct race proximate to, or identical with, the large elk of Alaska (*gigas* Miller). An independent subspecific status of elk in this region appears justifiable but the subject requires further study.

4. Ussuri elk, *A. a. cameloides* Miline-Edwards, 1867 (syn, ? *bedfordiae* and *bedfordi;* the name *americanus* is also applied to this form). Smallest form of elk, much smaller than the European *A. a. alces* from the European part of the USSR. Compared with western Siberia elk, it is not only smaller but stands lower on its legs, has a relatively larger head, and a lighter, more slender body. Body volume less. Body length of males (five animals) 250 to 276 cm (M 256), height at withers 172 to 195 cm (M 179), height at croup 170 to 180 cm (M 174), chest 173 to 180 cm (M 176), tail length 10 to 13 cm, and length of ears 22 to 24 cm. Maximum recorded weight of bull 400 kg (Kaplanov, 1948) but usually does not exceed 320 kg (Abramov, 1954); average weight probably only slightly more than 200 kg.

Skull measurements are generally smaller than those of European elk and the rostral region in the Ussuri form is relatively shortened. In structural features skull corresponds to that of *A. a. pfizenmayeri* (eastern Siberia type). Color uniformly dark while legs usually light-colored.

257 Antlers usually small and slender, without palmate portion, branched, dichotomously divided, circular in section, with large tines, usually symmetrical; in general antlers resemble those of deer. Number of tines in fully grown animals varies from two to four on each antler, reaching five in rare cases. Antler span 80 to 100 cm and weight 5 to 6 kg. Exceptionally (less than 2% cases), formation of rudimentary palmate section observed but area does not exceed 100 cm^2 (in western Siberia elk, 1,000 to even 2,500 cm^2; Kaplanov, 1948).

---

[249] Neither is an interrelation with American forms, at least the peripheral *americanus* and *gigas* acceptable (see below).

Found in the Ussuri and Amur regions in the north up to the Stanovoi range and the Lena watershed. In the west found roughly up to 123° E long. In the north along the Stanovoi range and near the sea much larger individuals occur and animals with palmate antlers, either intermediate to Yakutian form or representatives of latter forms have been reported. Elk of Sikhote-Alin are particularly typical.

Ouside the USSR occurs in northeastern China in the east, including the Great Khingan. References to a find in Khentei are erroneous as the animals living there are *A. a. pfizenmayeri.*

The form under description has been extremely well characterized and is sharply distinguished from all remaining forms of the species, especially the eastern Siberia *A. a. pfizenmayeri,* which has large antlers with palmate section. Combining the two into a single form (Flerov, 1952) cannot be justified.

The antlers of this form are of particular interest from the viewpoint of evolution of deer antlers. In other populations, especially in the western European part of the USSR, antlers without palmate sections are also seen, but in older animals. This feature in usually characteristic of underdevelopment and often associated with deterioration of a population or old age. The foregoing notwithstanding, such antlers are less massive and differ in structure from those of Ussuri elk.

The features of Ussuri elk are associated with their past distribution in the remote Manchurian-Chinese region. Evidently many primitive features are preserved in this form.

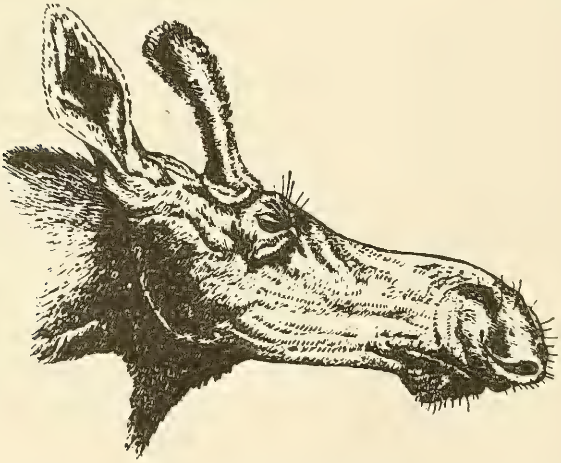


Fig. 78. Head of Ussuri elk (*Alces alces cameloides* M.-E.) (from Flerov, 1952).

In some parts of the range falling outside the USSR, i.e., in Eurasia, the animals resemble those in the Soviet Union. Several subspecies have been described from America but actually there are only two: *A. a. gigas* Miller, 1899 in Alaska, Yukon, and parts of British Columbia (largest of all the forms of the species with antler span running up to 200 cm) and *A. a. americanus* Clint., 1822 in the remaining parts of the American range. (V.H.)

Biology

Population. The following numbers of elk were recently counted in the territory of RSFSR (N.V. Eliseev):

1950 — 266,100	1956 — 353,000
1954 — 310,000	1960 — 480,000.

Supplementing these figures with data for Belorussia, Lithuanian Soviet Socialist Republic, Kazakhstan, and other republics of the Soviet Union, the elk population in USSR territory could number 500,000 animals. Data for the RSFSR are based on reports received from the Directorates of Hunting of various districts, territories, and 258 republics, which often determine elk population by counts (aerial and ground surveys), replies to questionnaires, or, rarely, general impressions. In some regions these figures are obviously exaggerated; it would therefore be more prudent to put the total strength of elk in the USSR at 400,000.[250]

There is no doubt that in the USSR the elk population at present is larger than at any time in the last 150 to 200 years. This is the result of a rise in numbers almost everywhere and tremendous expansion of the range, or more precisely, restoration of the former range over the past 20 to 30 years (see above). The elk population from 1928 to 1947 alone in some regions of the European part of the USSR rose on the average 10 to 15 times (Danilov, 1951; Dolgushin, 1953; Sludskii, 1950 and 1953; Nasimovich, 1955).

Data on elk populations in different regions have been given selectively because of the difficulty in obtaining complete information and in several cases because of its absence. In Belorussia in 1927 about 150 elk were counted (Fedyushin, 1929), in 1936—380 (Kulagin, 1940), and in 1952—600 to 800 (Serzhanin, 1955). Most elk

---

[250] Between 200,000 to 300,000 elk have been counted in Canada (early 1950's), 11,600 to 17,900 in the USA (1937 to 1948), 30,000 in Alaska (1946) (Peterson, 1955), 20,000 in Finland (1957), and 120,000 in Sweden. An average of 21,800 elk were caught annually in Sweden in the early 1950's (Sainio, 1956; and others).

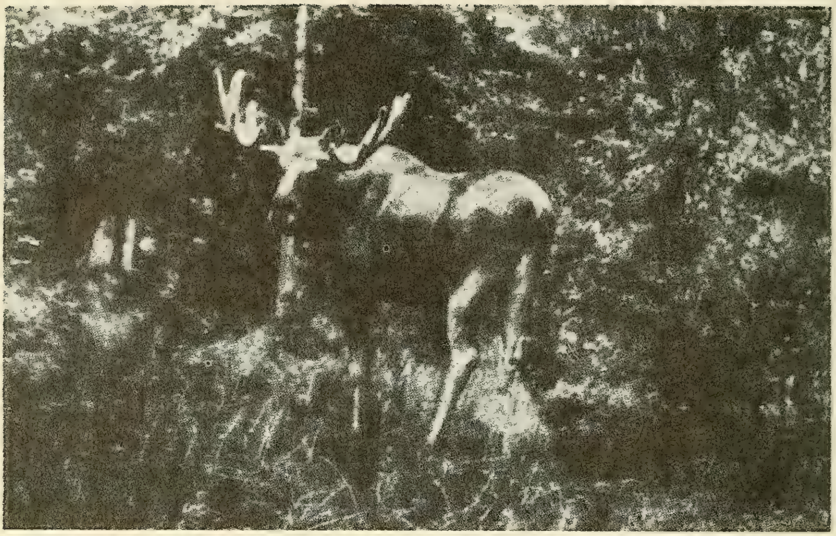


Fig. 79. Elk around Moscow, Zaveta Ilich station, Northern Railway. August, 1959. Photograph by T.V. Koshkina.

were in the Poles'e, Pinsk, and Viteb districts. In the northernmost Ukraine only a small number live a settled life; most are transgressors from Belorussia or RSFSR. The population on the whole is around 100. In the Baltic republics the maximum number of elk occurs in the Lithuanian Soviet Socialist Republic where there were 300 in 1939, 90 in 1948, and 400 in 1955 (Ivanauskas, 1957).

In the European part of RSFSR elk density per unit area is maximum in the central part of the range where mixed forests, and coniferous forests slightly more north, predominate. In the latter half of the 1940's the mean reserves of elk per 1,000 hectares of [mixed] forest area were 0.8 to 1.0, in the subzone of northern coniferous forests 0.6 to 0.7, and in the southern parts of the range where deciduous trees predominate and pine groves are scattered only 0.3 to 0.4 (Danilov, 1949).

259 The following examples provide some idea about the distribution of elk in the territory of Russian Soviet Federal Socialist Republic and partly also their population dynamics. In the Smolensk district in the winter of 1936 to 1937 there were 500 elk, which rose to around 1,500 by 1950 (Grave et al., 1951) and to 3,600 by 1954. In the Moscow district 200 animals were counted in 1929 (Yurgenson, 1935), 1,550 in 1944, 2,030 in 1946 (Danilov, 1947), and 9,000 in 1956 (Aleksandrova, 1957). In the Leningrad district in 1957 there were about 10,000 elk and in Pskov over 20,000 (N.V. Eliseev). In the

Vladimir district in 1954 there were 2,260 elk (Aleksandrova, 1957); in the Gorkii 1,720 in 1946 (Danilov, 1950); 4,250 in the Perm in 1941 (Danilov, 1949) later reaching 10,000 (Kuklin, 1946); in the Sverdlov in 1957 there were over 20,000 elk (N.V. Eliseev); in the Tatar Autonomous Soviet Socialist Republic in 1929 a total of 83 (Apisov, 1930), which by 1950 had risen to 1,318 and by 1954 to 2,400 (Aspisov, 1954). Some 25,000 elk were counted in the Arkhangel'sk district in 1951, which rose to 30,000 to 33,000 in 1954 (Semenov, 1957) but fell to about 25,000 in 1957 (N.V. Eliseev). The elk population in the Komi Autonomous Soviet Socialist Republic is quite considerable and slightly less in the Karelian Autonomous Soviet Socialist Republic.

In the latter half of the 1940's the average number of elk per 1,000 hectares of forest area in Siberia was placed at 0.4 to 0.5 (Danilov, 1949), i.e., only slightly more per unit area than in the southern parts of the range in the European part of the RSFSR. In 1957 in the Amur territory 12,000 elk were counted, 4,000 in Primor'e, 10,000 in Khabarovsk, over 8,000 in the Tuva Autonomous District,[251] and over 25,000 in the Yakutsk Autonomous Soviet Socialist Republic (N.V. Eliseev). In 1941 there were 7,500 in Tyumen and Kemerov districts together (Danilov, 1949).

The elk population continues to rise in the territory of Russian Soviet Federal Socialist Republic. By the early 1950's elk had become quite common in northern Kazakhstan; their occurrence was recorded in nine districts (Sludskii, 1953). Recently, a slight reduction in elk population has been noted in Kazakhstan.

Habitat. Within the Soviet Union elk inhabit almost every zone of the forest and are even found in forest-tundra, being confined there in winter to small spruce-larch forest islands in protected montane valleys (Polar Urals), willow thickets in swales and along the banks of rivers, and also birch and aspen groves (Dolgushin, 1953). At places in summer elk emerge into the open tundra, sometimes several hundred kilometers away from closed forest boundaries; some penetrate right up to the shores of northern seas. In winter the animals migrate southward into forest-tundra (Leble, 1953; Makridin, 1955; Gromov and Rapoport, 1938; Skrobov, 1958; and others).

Elk are fairly common in forest-steppes but confined mainly to islands of forests (deciduous[252] and pine) or marshy forests. Along river valleys small numbers of elk penetrate the steppe zone where they live along the banks of rivers and lakes overgrown with willow and appear in summer in sedge marshes, among reeds, and even in the open steppe 100 to 150 km from the southern boundary of permanent habitation (Sludskii, 1950; Danilov, 1951; and others). In Stalingrad region elk have been seen at the end of summer in the semidesert zone along banks of canals overgrown with willow, poplar, and maple (Stroganov, 1951).

---

[251] About 4,000 elk were counted at the end of the 1940's in the Tuva Autonomous District (Skalon and Shikin, 1950).

[252] In forest-steppes of the European part of the USSR elk are often encountered in oak forests with good reforestation, in young aspen groves (in winter), and also in plantations containing elm, maple, etc.

Thus the prevailing view that elk are purely taiga animals is incorrect. This view arose in the period when elk became nearly extinct in the central regions of the European part of the USSR. The fact that this animal reached the banks of Azov and Black Seas a few centuries earlier through river valleys was subsequently overlooked.

In addition to lowland forests, elk were earlier widely distributed even in montane taiga. Right up to the end of the eighteenth or early nineteenth century they also inhabited hornbeam and beech forests of the northern Caucasus and, in the even more distant past, of the western Trans-Caucasus (Vereshchagin, 1949; and others). In mon-
260 tane taiga elk prefer a relatively less rugged, gentle relief, and avoid steep slopes; broad valleys with abundant water sources or swamps represent particularly favorable spots. The vertical range of distribution is broadest in the eastern Altai and the Sayan ranges where the animal is found in summer right from the foothills to the upper forest boundaries (1,800 to 2,000 m). In the Altai they are also found on balds, especially at places where there are small lakes with swampy banks overgrown with willow and dwarf birch (Dmitriev, 1938). Thus in the Altai elk are found in summer roughly 2,200 to 2,400 m above sea level. They also occur above timberline in summer in the Sikhote-Alin mountains in tall grass meadows (up to 1,600 m; Kaplanov, 1948). In Lapland preserve about 5% of all elk counted occurred in montane tundras where the animal is confined to willow thickets (Semenov-Tyan-Shanskii, 1948). The forest boundary there runs at a height of about 350 m and elk ascend mountain slopes roughly to a height of 500 m.

Over a significant stretch of their range in the forest zone summer and winter habitats of elk differ sharply, but the animals visit during the greater part of the year willows along rivers, some types of deciduous forests with a tall herbaceous cover and fairly well-developed undergrowth, and also marshes overgrown with willow, dwarf birch, and pine.

In the warm period of the year, especially in summer, preferred habitats are those which have rich aquatic vegetation along water sources, whose banks are overgrown with willow, shrubs, or even a real forest. Among the habitats used regularly in summer are swampy alder groves and marshes (often overgrown with willow, birch shrubs or pine), especially if they are interspersed with small dry ridges overgrown with forests or adjoin large forests. In addition to water sources where elk feed on aquatic vegetation, other important summer habitats are mixed and deciduous forests with well-developed and fairly tall herbaceous vegetation. Other important habitats are young, burned-over and felled sections with luxuriant grass cover, areas with shoots of deciduous trees, and areas with abundant willow herbs [fireweed, *Epilobium*] (an excellent food for elk). The greater the variety of food sources, the more favorable the area for elk. In most dense forest masses with a uniform composition of trees elk are never numerous either in summer or winter.

Good shelter, offering protection from blood-sucking flies, is very important in the life of elk (see "Daily Activity"). Where elk are threatened by man in summer, they like to hide during the day in dense thickets of small forests, swampy alder thickets, or in dense coniferous saplings where their detection is difficult.

The winter distribution of elk is determined mainly by the availability of tree and shrub foods and also the thickness and density of snow cover in different biotopes in the latter half of winter. As far as possible, elk avoid sections with a snow cover of over 70 to 80 cm; in mountains and rocky sections shaded slopes with very loose snow are preferred. At places where elk are hunted the availability of shelters for protection from enemies are also of considerable importance.

Elk often use the banks of water sources as wintering sites, especially of rivers overgrown with willow, birch (in the north), and other deciduous species, growing burned-over and felled clearings, deciduous scrub woods (aspen and birch), and mixed and coniferous forests with dense undergrowths or numerous young trees. Elk often winter in pine forests rich in young trees (wintering of elk in such forests in the European part of the USSR has been observed from the farthest southern part of the range up to the Kola Peninsula inclusive) and in boreal forests (fir and spruce) with an abundant undergrowth of rowan [mountain ash], birch, goat willow, and others (Baltic, Leningrad, and Arkhangel'sk districts, Komi Autonomous Soviet Socialist Republic, the Sayans, Bureinskiy mountain range, Sikhote-Alin). Nut pine forests are of least importance; elk are found in them (eastern Siberia and Sikhote-Alin) only if other coniferous
261 and deciduous species are also present in large numbers. Larch (Larix) forests quite often serve as a habitat for elk in summer as well as in winter. Mixed forests are usually preferred to purely coniferous

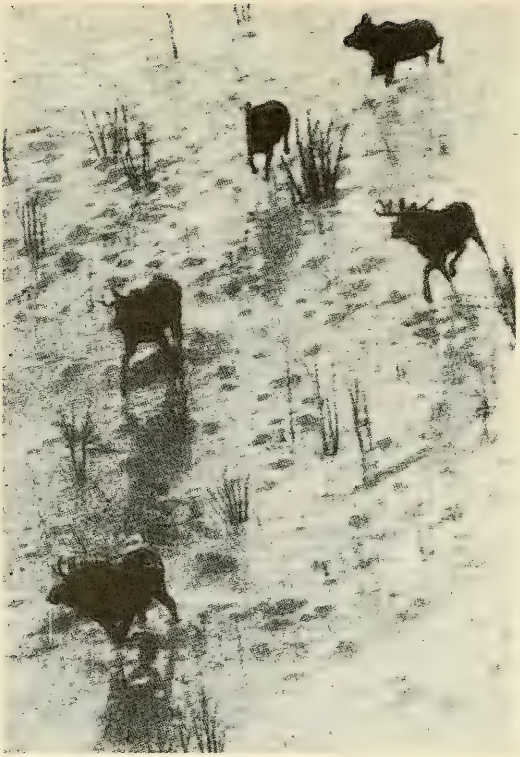


Fig. 80. Group of elk in Senchinsk marshes in upper course of Om' River, western Siberia. January, 1957. Photograph by K.T. Yurlov.

or deciduous. The only exception in this respect is young pine groves where large numbers of elk generally winter.

Elk are found in winter even in marshes, but only when these are extensively overgrown with willow and birch or, in the north, dwarf birch. Elk avoid marshy sections with ice crusts under the snow. The environs of marshes represent favorite haunts of elk in early spring in western Siberia (Dem'yanka River) since snow clears earliest in such areas (Kaplanov, 1935).

Depending on natural and other conditions, a particular habitat acquires special importance for elk. For example, in several regions of northeastern Siberia elk gather in winter in willow thickets along river banks (Zonov, 1931; Mikhel', 1937; Portenko, 1941; and others) or even congregate in overgrown burned clearings along the slopes of ridges where willow is abundant (Verkhoyansk badlands*; S.P.

---

*Literally, folded lands—Sci. Ed.

Naumov). The winter habitat of elk in the basin of the Chul'chi River (eastern Altai) at a height of 1,400 to 1,700 m is highly typical; there, the animals are mainly confined to broad mountain valleys overgrown with round-leaved birch *(Betula rotundifolia),* in the proximity of the edge of deciduous or mixed forests with an abundant undergrowth of shrub birch (*Betula humilis*). Aspen, mountain ash, and birch, common in much of the winter habitat of elk, are almost absent in the composition of these local forests (Dmitriev, 1938).

No less characteristic is the habitat-related distribution of elk in Sikhote-Alin. In summer elk are confined mainly to coniferous forests (nut pine-spruce-deciduous and larch) but also move into the floodplains of rivers, marshes, the upper portions of mountains in tall grass meadows among plantations of rock birch (*Betula ermani*), and also in grassy-spruce forests. In winter the maximum number of elk occurs in open larch and spruce-larch forests and in boreal forests with deciduous underbrush (Kaplanov, 1948).

Often males are distributed in very different habitats from those of females with calves. For example, males locate in summer mainly in the upper courses of Altai rivers near timberline and on balds, while females with calves are common along lower slopes (river valleys and forest lakes) (Dmitriev, 1938). Only some adult males and females without calves remain in the watershed regions of Pechora-Ilych preserve, which is covered by pine groves, in the latter half of winter. The majority of elk and all females with young are confined to river valleys with willow thickets, since on the ice of
262 rivers there is less snow than in the watershed regions (Teplov and Teplov, 1947). In Lapland preserve females with calves winter in the least snowy sections; only males and females without calves locate in areas where the snow is greater (Semenov-Tyan-Shanskii, 1948). The wintering sites of males in Sikhote-Alin are usually located at higher elevations than those of females (Kaplanov, 1948).

Food. Within the Soviet Union elk, according to Danilov (1958), feed on 149 genera of angiosperms (110 genera of herbaceous plants and 39 genera of trees and shrubs). They also eat 5 or 6 genera of gymnosperms (pine, juniper, yew, and others), no less than 5 genera of pteridophytes (except for horsetail, others are seldom eaten), 3 to 4 genera of lichens (mostly epiphytic and rarely the terrestrial *Cladonia*), 11 genera of fungi, several genera of algae (laminaria, *Conferva,* and others), and sometimes even mosses. In all elk utilize as food up to 175 genera of plants, representing no less than 250 species. This subject has been variously studied in different regions but by and large data are scanty.

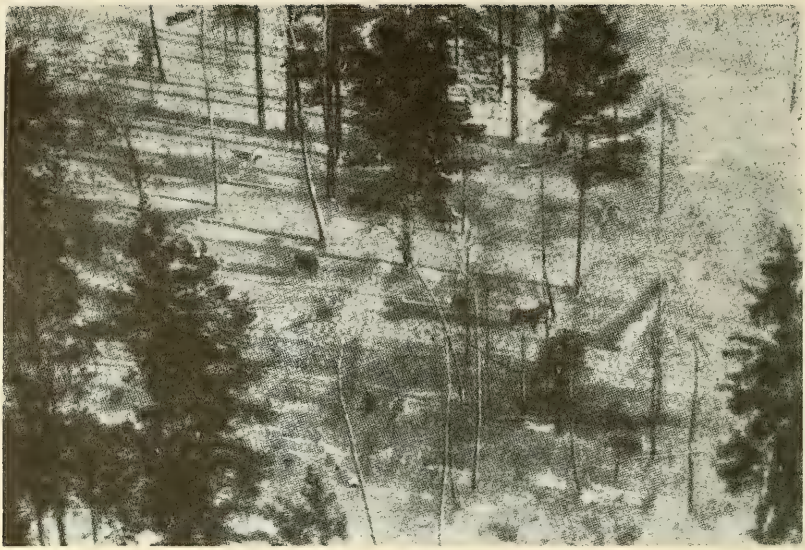


Fig. 81. Winter habitat of elk in a felled section of Pri-Ob' pine forests. Novosibirsk region. January, 1957. Photograph by K.T. Yurlov.

In Mordov preserve observations on two pasturing domesticated elk established that in the summer–autumn period they feed on 133 species of plants, of which 61 constituted principal food items (Shaposhnikov, 1951). In Priok-Terras preserve (Serpukhov region of Moscow district) elk in summer eat no less than 62 plant species (Aleksandrova and Krasovskii, 1957). In Lapland preserve elk use no less than 47 plant species, of which 14 constitute primary food items (Semenov-Tyan-Shanskii, 1948). In Oka preserve (Ryazan' district) in the summer–autumn period alone elk eat 46 species (Borodin, 1940), and in Sikhote-Alin 43 species[253] (in summer—32, of which 6 are primary; in winter—28, of which 11 are primary; Kaplanov, 1948). For Belorussia, on the whole, 38 species have been identified (Sablina, 1955; Serzhanin, 1955), and for Zhiguli in summer 33 species (Zharkov, 1954). Information is much more scanty for other regions of the country.

263 Seasonal variations in food are distinct among elk. In summer the main food is represented by herbaceous plants, among which many are aquatic, grow around water bodies, and in general flourish

---

[253] According to Abramov (1954) Far East elk consume over 90 plant species but the author has actually identified less than 30, all of which were previously identified by Kaplanov (1948).

in moist habitats. Among other herbaceous plants elk avidly consume relatively tall plants (willow herbs [fireweed] are a particular favorite), sticky-leaved spirea, buckbean, buttercup, sweetflag, horsetail, *Nuphar,* water lities (not only the green portions but also the rootstock), and many others (calla, cat-tail, *Sagittaria, Alisma, Potentilla,* loosestrife, dandelion, sorrel, some Umbelliferae, etc.). Information on these plants comes from a relatively small number of places in the range.

Over much of the range (Kola Peninsula, Arkhangel'sk region, Komi Autonomous Soviet Socialist Republic, Rybinsk reservoir region, Altai, and Yakutia) sedge is utilized quite well but mainly in spring and early summer. The role of grasses, especially low ones, not only in the Soviet Union but also in America (Peterson, 1955), is not generally important in the diet of elk. Taller grasses at times are consumed in large quantities in the southern parts of the range (Tula abatis [stockade], Mordov preserve, and Zhiguli) and at places in the north (Rybinsk reservoir). For example, in the stomach of an elk caught in Tula abatis in mid-August, grasses predominated: reed grass, bent grass, meadow grass, hair grass, etc. (Likhachev, 1957). Elk in Zhiguli grazing sites consume in August about 90% giant fescue plants (Zharkov, 1954). In Mordov preserve five types of grasses serve as primary food items (Shaposhnikov, 1951). In Priok-Terras preserve sedges, leguminous plants, and grasses are almost untouched by elk (Aleksandrova and Krasovskii, 1957).

On the whole elk are quite adaptable and probably less fastidious in their choice of food[254] than some other ungulates. Elk can live and reproduce in habitats even in the absence of such important summer foods as aquatic plants (Zhiguli). In this case the absence of some food plants is evidently compensated by the presence of others. For example, in Zhiguli those consumed avidly from May through August are *Aegopodium, Crepis,* and *Bupleurum* (Zharkov, 1954). These plants are usually not known as food of elk in other parts of the range.[255] In the diet of Ussuri elk 25 to 30% of the plants utilized as food belong to the Manchurian floral complex (Kaplanov, 1948; Abramov, 1954); in other parts of the range these varieties of plants are absent. With migration from one area to another, the food composition of elk also changes notably (Shaposhnikov, 1951; Likhachev, 1957).

---

[254] Based on observations of grazing domesticated elk, Shaposhnikov (1951) came to the conclusion that the food composition largely depended on the degree of plant abundance. This conclusion is extremely debatable and is not in conformity with the winter observations of the same author (see below).

[255] In Mordov preserve *Aegopodium* is considered a secondary food (Shaposhnikov, 1951).

In summer trees and shrubs, mainly leaves and green shoots, are commonly used as food to a much lesser extent than in winter. Quite often elk do not eat the branches completely, tearing off only the leaves by running the branch through their mouth. Among conifers elk eat only young pine shoots in summer (Dem'yanka River in western Siberia; Rybinsk reservoir). Elk eat leaves of aspen,[256] mountain ash, some species of willow, and buckthorn best (mainly in autumn, together with fruits). They also consume well bird cherry, oak, and some species of birch, at least in some periods of the vegetative season. Moreover, they consume well in some regions for at least part of the summer period, leaves or shoots of maple (Zhiguli and Sikhote-Alin), raspberry (Belorussia, Mordov preserve), linden
264 (Mordov preserve), ash (Belorussia), *Euonymus* (Zhiguli), elm, dog rose, blackthorn, spirea (Buzuluk pine forest), etc. It is interesting that in Priok-Terras preserve elk are not at all attracted to oak, *Euonymus,* and linden in summer. There are references for other regions where *Euonymus,* linden, and other species are poorly or not at all consumed by elk.

Herbaceous plants and trees are generally consumed throughout summer to various degrees, but aquatic plants are consumed well throughout the warm period from the time they begin to grow well (end of May to early June) until the end of September or even October inclusive. Terrestrial herbaceous plants are consumed in a definite sequence, since they grow at different times, and the animals prefer tender green portions and parts which at a given time are more nutritious: the first shoots, tender leaves, and stalks in spring and early summer, and flowering shoots in the latter half of summer, i.e., the upper portions of stalks with bud, ovaries, and flowers (Shaposhnikov, 1951; Zharkov, 1954).

In Zhiguli in May herbaceous plants account for about 79% of the entire intake and shoots with tender leaves, sharp-leaved maple, and bird cherry the remaining 21%. Leaves of *Aegopodium, Bupleurum,* grasses, and chervils [cow parsley] constitute the basic food. In June-July the intake ratio of herbaceous food to tree food remains the same (80 to 20%), but along with *Aegopodium* and *Bupleurum,* leaves of *Crepis* and spirea are also well consumed. In August the proportion of tree foods increases to 40% (up to 90% terminal shoots of oak and 81% willow). Flowering shoots of over 10 species of plants are eaten well—up to 88% *Bupleurum*, 83% fireweed, 74% *Crepis*, and 50% broad-leaved bluebells, etc. (Zharkov, 1954).

---

[256] The stomach of an elk killed in August in the basin of the Northern Dvina was filled with aspen leaves (Yurgenson, 1935).

Similar shifts in the composition of the food intake of elk have also been traced in Priok-Terras and Mordov preserves and in many other regions. In Mordov preserve over most of the summer a marked diversity in the food consumed is evident and no perceptible preference for particular species discernible. In spring and autumn the food composition is less diverse (in August about 50 plant species, in September–October about 20, and in November, 6) and a few plant species predominate during these periods of the year (Shaposhnikov, 1951).

In Lapland preserve the main food in spring (end of May to first half of June) is represented by fresh leaves of willow, birch, and mountain ash. From July considerable quantities of fireweed, spirea, sedge, marsh horsetail, buckbean, *Nuphar*, etc. are consumed. In September herbaceous vegetation predominates and in October mainly tree food. The summer food intake is quite extensive, the items widely dispersed, and only some plant parts, mainly the upper portions of herbaceous plants, nibbled (Semenov-Tyan-Shanskii, 1948).

Secondary foods of elk in the warm period, not consumed universally but fairly rarely, include algae, ferns (in Mordov preserve bracken and ostrich feather ferns are well consumed by tame elk), tops of reeds, and most berries. On the other hand stalks and leaves of berry shrubs (bilberry, mountain cranberry, and blueberry) are quite well consumed. In September and October some acquire nearly as much importance as primary foods (Belorussia, southern Karelia, Arkhangel'sk region, Komi Autonomous Soviet Socialist Republic, and Sikhote-Alin). In Mordov preserve in the last ten days of October leaves and stalks of mountain cranberry have comprised 42.5% of the food intake and bilberry 15.2%. The proportion of mountain cranberry in November was 42.3% (Shaposhnikov, 1951).

265 In Mordov preserve tame young elk at the end of summer and in autumn consume nearly 15 species of mushrooms (including fly agaric). In the first ten days of October about 20% of the food intake is accounted for by mushrooms (Shaposhnikov, 1951). Mushrooms are avidly consumed by elk in the Pechora basin (Turov, 1953) and in the southern part of the Far East (Abramov, 1954). Similar observations for other regions are absent; some researchers (Cherkasov, 1884) contend that elk do not eat mushrooms. Only a few have recorded the consumption of mushrooms in Canada (Peterson, 1955). The intake of mushrooms by elk is quite well known in Sweden (Skuncke, 1949). Evidently elk respond differently to mush-

rooms in different parts of the range. Herbaceous plants consumed by elk comprise some poisonous ones and some of medicinal value (in Priok-Terras preserve lily-of-the-valley is eaten well). Buckbean and calla possess anthelminthic properties (Rykovskii, 1957).

In winter tree and shrub vegetation, mainly branches, and most needles of coniferous plants represent the main food of elk. In the early, less snowy period of winter, and sometimes throughout winter in the southern region of the range, deciduous varieties play the main role, while the importance of conifers perceptibly increases in the latter half of winter.[257] Contrary to the highly nutritious food to which elk turn in summer, tree food is essentially supportive in winter. Elk survive on tree food for six to eight months, for a shorter period in the southern part of the range, and a longer period in the north where winter is more prolonged. Elk are better adapted to such foods than the overwhelming majority of ungulates. The Evenkian allegorical names for elk are quite apt: "moota" (tree eater) and "shektata" (willow eater). For superstitious reasons Evenkians while hunting avoid using the common word for elk, "toka" (Podkamennaya Tunguska River; Suslov, 1927).

The range of trees and shrubs consumed by elk in winter is extremely broad—no less than 50 genera[258]—of which roughly one-fourth form the main diet in one region or another. In some parts of the range relatively few play a major role: in the northern part and in typical taiga regions not more than 4 or 5 genera, in the central regions of the European part of the USSR (Moscow and others) 6 to 8, and in the same area but in the zone of broad-leaved forests and forest-steppes 10 to 12. In Sikhote-Alin elk readily consume 8 to 10 species of tree species.

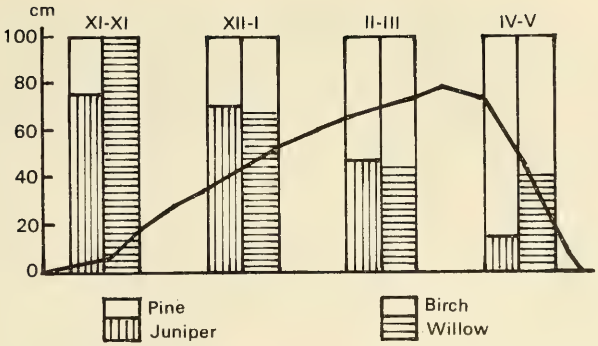
In a given region not more than half of the total number of trees available constitute primary food at a given time. This is especially true of regions in which the latter half of winter is extremely snowy and access to low shrubs is greatly hindered. For example, in Lapland preserve in the latter half of winter elk rarely consume
266 small willows and junipers which are normally their favorites (Fig. 82), but feed mainly on branches of birch and pine needles (Semenov-Tyan-Shanskii, 1948).

Among the tree and shrub species of importance to elk in winter as primary food in much of the range in the USSR are willow,

---

[257] At places where the population density of elk is high and deciduous forests few, pine is quite often intensely attacked even from early winter.

[258] It is not precisely known which species (highly numerous) of willow, birch, and pine are consumed by elk. Still, the intake of different species of a given genus varies notably.



265 Fig. 82. Ratio between intake by elk of preferred twigs (willow and juniper) and principal (birch and pine) food in relation to height of snow cover. Lapland preserve (from Semenov-Tyan-Shanskii, 1948).

Note: Roman numerals refer to calendar months.

pine[259] (especially prominent is the role of saplings and young trees up to the age of 15 to 25 years), aspen, and mountain ash. Birch is eaten equally extensively but less avidly; however, at places where aspen and mountain ash are few (northern parts of the range) birch is considerably more important than the other two species. In a very limited part of the range species important as primary food are juniper (some taiga regions of the European part of the USSR), fir[260] (Pechora basin, Urals, Irkutsk region, and Amur zone), bird cherry (many regions of the European part of the USSR and Sikhote-Alin), maple, oak, and willow (southern parts of the range within the European part of the USSR; in Sikhote-Alin maple also). Buckthorn and warty-bark spindle tree are well eaten (central and southern parts of elk range within the European part of the USSR) but not abundant everywhere; hence they do not constitute primary food items though highly preferred by elk. In this same category belong currants (a few varieties) and raspberry, which are eaten well but usually limited and, moreover, quickly covered with snow. In a few regions alder, linden, and hazel nuts are consumed satisfactorily, but rarely. Species such as poplar, honeysuckle, acacia, dwarf birch, rhododendron, and yew (rare everywhere) are usually not significant for elk. Almost everywhere spruce is eschewed; its consumption by elk usually serves as a reliable index of an unfavorable food situation.

---

[259] In America pine is hardly touched (Peterson,1955).

[260] Fir *Abies balsamea* (absent in the USSR) is an important winter food of American moose in eastern Canada (Peterson, 1955).

The uneven intake (sometimes from excellent to total rejection) of a given plant species in different parts of the range may be due to the differences in their chemical nature and morphology, as well as the degree of abundance and accessibility of other, more preferred foods. In forests adjoining Oka preserve, at places where there are many elk, pine is usually the main food (100%). Young trees are often completely destroyed, 76% have broken tops, and up to 20% wither away. In forests where elk are few and food more readily accessible pine is eaten much more rarely as elk prefer aspen, mountain ash, gray willow, and buckthorn over pine (L.P. Borodin). Pine and birch represent main and bulk food; although compulsory they are nowhere preferred as food by elk in most regions.

A good idea of the food selectivity of elk is provided by comparative data on tree species consumed by them and the availability of those species in forests (Table 1).

In winter elk damage shoots of deciduous trees and shrubs (up to 20 to 30 cm long and 5 to 12 mm thick at the bite point); in the case of coniferous plants, needles and rarely shoots are consumed. During below-freezing weather, bark is poorly eaten and, for example, in the north at temperatures under –2°C bark is almost untouched (Fig. 83). In the southern parts of the range where winter is very mild and thaws frequent, bark on the southern side of trunks is warmed by insolation even on frosty days and thus consumed throughout winter in large quantities. For example, in the Tula abatis, according to Likhachev (1939), bark is the most important constituent of the winter diet of elk. The importance of bark is particularly discernible in transitional seasons of the year (spring and especially autumn); its consumption is far higher in those months than at any other time of the year. In summer elk rarely touch bark. Sometimes they eat only shoots (of birch, hazel nut, spindle tree, etc.) or, contrarily, consume only bark (of spruce in Pechora-Ilych preserve). The main form of damage caused to pine by elk in Moscow region is the breaking of tops of young pines up to the age of 20 years (59%), gnawing of bark (34%), and consumption of shoots (7%) (Dinesman, 1957).

267 Under conditions of food scarcity, especially in the latter half of winter, elk consume large quantities of arboreal lichens (*Bryopogon, Usnea,* etc.). In an elk killed on November 19 at Sikhote-Alin, arboreal lichens constituted over 50% of the stomach contents (Kaplanov, 1948). Sometimes elk rake the snow with their muzzle (not more than 20 cm deep) to gather tiny berry shrubs, shoots (most often sedge), or even terrestrial lichens. In larch forests in Sikhote-Alin consumption of mountain cranberry in one case amounted to

TABLE 1. WINTER FOOD CONSUMPTION OF ELK IN PINE FORESTS AND SUCCESSIONAL BURNED-OVER FOREST SECTIONS IN MORDOV PRESERVE (5 HECTARES; 13,416 TREES AND SHRUBS; JANUARY, 1946; FROM SHAPOSHNIKOV, 1951)

Species of trees and shrubs	Percentage in plantation	Importance as food (% of total bites)	Degree of utilization of reserves (%)	Average number of bites per tree
Pine	52.1	36.5	51.0	2.9
Aspen	18.2	33.2	97.6	3.9
Birch	7.0	5.5	54.0	3.0
Linden	6.5	0.4	6.1	2.6
Broom (*Citiscus ruthenicus*)	5.5	3.5	39.7	3.1
Mountain ash	4.7	9.0	100.0	4.1
Goat willow	2.3	3.7	96.5	3.8
Buckthorn	2.0	4.5	100.0	4.5
Warty bark spindle tree	1.4	4.0	100.0	6.6
Spruce	0.13	—	—	—
Oak	0.07	0.1	100.0	5.0
Total (on the average)	100.0	100.0	61.0	3.4

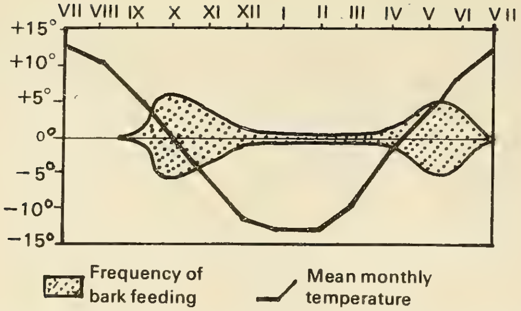


Fig. 83. Intake of tree and shrub bark by elk depending on atmospheric temperature. Lapland sanctuary (from Semenov-Tyan-Shanskii, 1948).

Note: Roman numerals indicate calendar months.

31.5% (Kaplanov, 1948). By and large, however, digging food up from under snow is not typical of elk.

Male elk consume in winter up to 9 kg of food (air-dried), female elk about 6 kg, and juveniles up to 5 kg (Semenov-Tyan-Shanskii, 1948). According to experimental data obtained in Alaska an elk of mean annual weight of about 550 kg requires 16 kg of food (air-dried) every day (Palmer, 1944). Adult elk in Pechora-Ilych preserve in summer consume 30 to 40 kg green fodder (not air-dried) per day, in the first half of winter up to 15 to 20 kg, and in March–April, i.e., during the "yarding" period, 6 and not more than 8 to 12 kg (Knorre, 1952 and 1953).

In winter the water regime of elk, like that of most other ungulates, is extremely thrifty. The animals lick very little snow since it is associated with loss of heat in the organism (Kaplanov, 1948). Feces are dry and urination extremely rare, sometimes only once a day (Semenov-Tyan-Shanskii, 1948).

268 Elk do not visit natural salt licks over much of the range (European part of the USSR,[261] western Siberia, Altai, and the Sayans). In Irkutsk district visits are rare (Kopylov, 1950), while in Yakutia, Amur, and Sikhote-Alin natural salt licks are well-used in the snow-free period of the year (Belyk, 1948; Kaplanov, 1948; Abromov, 1949). From time to time the animals go to salt licks in winter also (Sikhote-Alin). In Sikhote-Alin elk lap turbid water and muddy the soil, especially around sedge root tussocks.[262] In addition to water-

---

[261] In the northern Urals elk in spring and summer go to some definite places in marshes where they lap stagnant water with a rusty bloom (Turkin and Satunin, 1902).

[262] When mineralized waters rise to the surface around roots of sedges, salts are evidently precipitated (Kaplanov, 1948).

logged solonetzes they also visit marshes (to swallow "liquid peat") and dry salt licks where they lap viscous clayey soil and the weathering crust of tuff; in these environs they eat sphagnum moss (Kaplanov, 1948). On marine coasts of the Primor'e territory elk consume laminaria and other algae which are rich in salt, lick salt-coated stones, and lap sea water (Abramov, 1954). In several regions of the USSR elk visit artificial salt licks. In winter in eastern Siberia and other regions of the USSR elk avidly lap water rich in organic compounds brought to the surface at places by cryoturbation.

A mineralogical analysis of the composition of salt licks has not provided a satisfactory explanation as to why elk visit them (Peterson, 1955; Yu.A. Liverovskii).

In captivity elk eat cabbage, root crops, potatoes, and other cultivated plants.

Home range. Except during the period of rut, when males without females wander extensively, and the period of autumn–winter and spring migrations, which do not occur everywhere, elk lead a fairly settled way of life, remaining long within a given locality. In summer the individual home range of an elk is more extensive than in winter, but if the animal has occupied from spring onward a home range close to water sources, rich in food, and free from danger, it spends the entire summer there; migrations in such cases are minimal (Kaplanov, 1935). When the population density is high, boundaries of individual home ranges overlap because elk possess no "defended territory" from which other animals are driven away. The only obvious exception is the female, which during the first few days after calving will allow no other elk nearby.

In Sikhote-Alin preserve in summer elk move several kilometers to salt licks but do not travel daily. As many as 28 elk have gathered at a single salt lick at one time (Kaplanov, 1948). When salt licks are absent such extensive movements of elk outside the limits of their permanent habitation are atypical. In the period of rut elk live in pairs in a given area (Kaplanov, 1935; Semenov-Tyan-Shanskii, 1948); their daily movement in general is 5 to 6 km. Single males sometimes wander several tens of kilometers daily in search of a female (Knorre, 1953).

In winter, as the snow height increases, daily wanderings of elk decrease concomitantly. In March, when the snow cover is 65 to 70 cm high, daily wanderings are limited to 700 to 900 m. In Lapland preserve in early March an adult male elk in a pine forest did not move from its 10-hectare home range for five days; a large number of animals settled for an even longer period (Semenov-Tyan-Shanskii, 1948). In the Dem'yanka basin a group of three or four elk in the latter half of winter daily traversed 1 to 3 km or sometimes even more; only frightened elk move tens of kilometers or more (Kaplanov, 1935). In the Pechora basin elk are equally static in winter. Herds remain for days in an area of a few hectares when the snow cover is high. Individual yards there are quite dispersed (Teplov and Teplov, 1947).

In Darwin preserve, when the snow height is 40 cm at the end of January, females and fawns move daily about 500 m in a pine-aspen forest outside a territory of about 2.5 hectares (Nasimovich, 1955). In Voronezh preserve the daily wandering of a male elk which fed in
269 early December on river banks was 800 m (Nikul'tsev and Predtechenskii, 1957). Similar data on the low mobility of elk in winter, especially in the period of "yarding" during deep snow, have been recorded for Leningrad district (Sablinskii, 1914), Buzuluk pine forest (Knorre, 1939), and several other areas.[263]

In summer elk are widely distributed but gather into herds in winter at a few places where food is more abundant and snow less. In Lapland preserve in a forest area of 1,000 hectares the average density of elk in 1940 was 0.8 and in 1941, 1.0. In yards, however, the corresponding values for 1,000 hectares were 3.7 and 4.6, i.e., almost five times greater (Semenov-Tyan-Shanskii, 1948). In Mordov preserve in the mid-1940's, in spite of a high overall density of ungulates, elk occupied in winter only 39% of the territory of the preserve (Kozlov, 1947).

Indices of elk population density in different parts of the Soviet Union have already been given (see the section "Population"). In the latter half of the 1940's these varied on the average from 0.3 to 1.0 per 1,000 hectares (Danilov, 1949). At places where elk are protected and food still available, population density may be much higher—up to 20 to 25 animals per 1,000 hectares (Oka preserve, 1945[264] and Priok-Terras preserve, 1952 to 1955). Experience has shown, however, that under these conditions, forests are greatly damaged, winter food soon exhausted, and the elk population in subsequent years smaller (see "Population Dynamics").

Daily activity and behavior. In summer elk are active during the day, mainly in the first two or three weeks of June. With the appear-

---

[263] According to Semenov-Tyan-Shanskii (1957) the average daily wandering of elk in Arkhangel'sk district with a snow thickness of 80 to 120 cm was 3.5 km, going up to even 3.9 km for some individuals in the herd. Obviously contradictory to this is mention of the habitation of individuals in an area 1.9 km × 0.8 km (152 hectares). Some errors have evidently crept into the author's data.

[264] In some sections of Oka preserve the population density of elk has reached 34.5 per 1,000 hectares (L.P. Borodin).

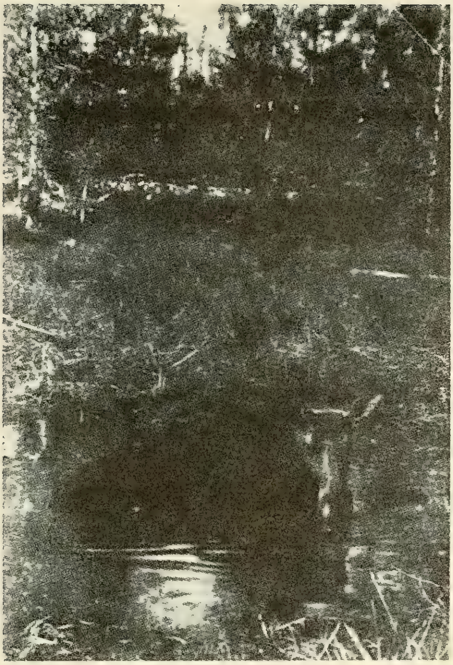


Fig. 84. Female elk in resting place in water. Position of head with nostrils touching the water to avoid possibility of attack by gadflies is characteristic of elk. Elk farm of Pechora-Ilych preserve. July, 1959. Photograph by E.P. Knorre.

ance of a large number of gadflies and horseflies and high daytime temperatures, elk take to a nocturnal mode of life. During the day they lie up in quiet, cool places where the wind blows strongly and blood-sucking flies are few. In montane regions they often ascend slopes (Sikhote-Alin, Altai, and southern Urals), emerge into open
270 zones and large clearings, and move above tree line. Quite often, for example in close proximity to populated areas, elk remain hidden during the day in thickets of young coniferous plants, in swampy alder thickets, and among shrub thickets. At places of little disturbance they remain during the day in open swamps, along shores of lakes, and in shoals and river spits, often lying in shallow water and at times advancing into water up to their neck. In the warm period elk like to remain in wet places; when the spot heats up the animal shifts to a new place.

In the period of mass flights of horseflies elk in Pechora-Ilych preserve remain in their beds for about 60% of the day versus slightly more than 50% in the period when horseflies are absent (I.S. Turov, 1953). However, even at places where horseflies are negligible

(Lapland preserve) elk remain lying for long periods in summer (Semenov-Tyan-Shanskii, 1948). Evidently the animals are troubled during the day not only by horseflies but also by high air temperature, which confirms observations made on captive elk (Knorre, 1953).

In summer elk emerge for feeding when twilight sets in and the heat has diminished, returning to their beds not later than 6:00 or 7:00 a.m. They feed in burned-over sections, in bank-side shrubs, marshes, and often in water bodies in which they sometimes spend much of the day. Elk like old river channels with stagnant pools thickly overgrown with dense aquatic vegetation, small streams, and shallow bays of lakes. The animals get at aquatic vegetation by submerging their head under water (for 20 to 60 sec; Denniston, 1956). In shallow places they prefer to feed with their ears above water. In deep waters they sometimes dive for food (Cherkasov, 1884; Petri, 1930; Dmitriev, 1938; and others). Instances are known of American moose diving to a depth of 5 m and remaining under water for 50 sec or more (usually not more than 30 sec) so that even the ripples on the surface had vanished. Feeding on aquatic vegetation continues uninterruptedly for 30 to 60 min, followed by a prolonged interval during which the animals stand in water or even leave it. Sometimes they recommence feeding within 10 to 15 min, however (Peterson, 1955).

Elk visit salt licks at night and, if not threatened, in the evening or morning as well. They visit nearby salt licks daily, as many as seven or eight times during the night (Peterson, 1955). They do not go to distant salt licks every day but remain close to them, often for several days (Sikhote-Alin). In a salt lick elk suck water and semifluid mud through their lips for 10 to 15 min or even an hour almost uninterruptedly. They subsequently feed or lap clean water (Kaplanov, 1948).

Elk easily swim for a few kilometers. They periodically visit islands in lakes, remaining 2 to 3 km away from the shore. In Lapland preserve 12% of the summer occurrences of elk were animals swimming through the lake (Semenov-Tyan-Shanskii, 1948). The rate of quiet swimming of an elk is about 2 km an hour[265] (Kaplanov, 1935). Instances are known of elk swimming across Rybinsk reservoir, a distance of 20 km. Similar distances have been reported for Scandinavian and American moose (Peterson, 1955).[266]

---

[265] Reindeer during migrations swim through rivers at a speed of about 5 km an hour.

[266] References occur in literature to instances of elk swimming across the Gulf of Bothnia (Kalnin'sh, 1950).

271 Fig. 85. Swimming elk. Deep lake, Moscow district. November 7, 1958. Photograph by V.D. Lebedeva.

Elk cross a marsh by the shortest route, selecting places where land masses rise sharply or where "islets" or ridges occur (Kaplanov, 1935). Buturlin (1934) has emphasized the surprising ability of elk to move through marshes; in swampy places the animal crawls on its belly with its forelegs stretched out in front. Tarasov (1956) thinks elk are better equipped to negotiate marshes than reindeer. In the Altai elk cross marshes along definite tracks, stamping out deep trenches 50 to 70 cm in depth in drier parts (V.G. Heptner).

271 Elk in general are quite sluggish. They avoid running without purpose and walk with a long stride, covering without difficulty 1.5 km in 10 min. Elk running alongside automobiles can gallop for a few hundred meters at a speed of up to 35 or even 55 km an hour (Peterson, 1955). The speed of an elk in a fast trot without special haste is 15 to 16 km an hour (Buturlin, 1934). Elk jump less well than other ungulates, clearing a fence 2 m high by thrusting their forelegs upward and tumbling heavily on the other side, usually breaking the fence in the process.

To get at food on the ground elk usually have to spread their forelegs widely or even go down on their knees. While eating fungi, sorrel, red bilberry, and lily-of-the-valley young elk often crawl on their knees (Shaposhnikov, 1951; Skuncke, 1949). Adult elk particularly enjoy browsing the tops of relatively tall herbaceous plants.

In the period of rut elk are active throughout the day. In winter they lie down several times and feed several times as well. Early in winter adults lie down four or five times a day and at the end of this season, when snow is heavier, eight or ten times. Young animals lie down somewhat more often than adults (Semenov-Tyan-Shanskii, 1948). In the Dem'yanka River basin the periods of rest and feeding in winter alternate five to six times in a day (Kaplanov, 1935).

In Komi Autonomous Soviet Socialist Republic during below-freezing weather elk remain in their bed for 75 to 80% of the night and 35 to 40% of the day. At a temperature of [minus]* 40 to 50°C elk lie down for several hours deeply entrenched in porous snow, above which only the withers and head are visible; heat dissipation is thus minimized (Knorre, 1953). The opinion that elk are more active during cold weather than at any other time (Buturlin, 1934; Abramov, 1954) is evidently incorrect. It is highly probable at the same time that where persecuted by hunters the rhythm of activity is shifted into nocturnal hours. According to Kaplanov (1935) in winter elk are more active at night than during the day. In strong winds and snow-storms elk rest anywhere under a shelter and gather in thickets of young coniferous plants.

At the time of feeding elk spend more time motionless, plucking branches and needles, than they do walking; no more than 2 hr a day are spent in moving through snow 60 to 65 cm deep. In Lapland preserve, when the snow cover is 50 to 90 cm deep, elk feed on branches and needles of a single tree or bush roughly five times more intensely than at the beginning of winter when the snow is no more than 10 to 12 cm deep (Semenov-Tyan-Shanskii, 1948). While feed-
272 ing elk quite often break up small trees by seizing the top in their mouth and bending the trunk by moving forward. The track of the animal is invariably away from the tree (Semenov-Tyan-Shanskii, 1948). Yet many authors state that the animal breaks the tree by throwing its chest heavily against it and passing the trunk between its legs.

The weight load on the hooves of elk is considerable while walking and, depending on the method of calculation, ranges from 322 to 749 g per cm^2 (Table 2) (E.P. Knorre; Pechora-Ilych preserve). The weight load is reduced to one-half when the animal rests, standing on its hooves, or while moving over snow and in marshy soil. Nevertheless elk do get stuck deep in snow, almost to the ground or at least to two-thirds of the snow thickness. However, elk movement on snow is greatly facilitated by its massive build and long legs.

---

*Omitted in Russian text—Sci. Ed.

272 TABLE 2. WEIGHT LOAD ON TRACK OF ADULT PECHORA ELK (IN g PER cm^2 OF HOOF SURFACE)

Sex	Month	With no allowance for additional support area	With allowance for additional support area
Male	October	749	434
Male	March	624	270
Female	July	762	322

In the Kola Peninsula adult elk negotiate without difficulty a porous snow cover 40 to 50 cm deep. A snow cover of 60 to 70 cm usually compels elk to move on old tracks, but if the snow is porous the animals can run in it without particular difficulty. Under such snow conditions young elk walk in the tracks made by adults. When the density of snow cover is 0.20 to 0.22 and the height 85 to 90 cm, running adult elk push the snow with their belly and move with great difficulty (Nasimovich, 1955). A snow cover of 90 to 100 cm is
273 critical for elk; in such snow, especially with a frozen crust, wintering conditions become somewhat difficult. Yet even then, if seldom threatened by hunters, elk winter well. In regions where hunting is more intense the animals prefer places where the snow cover is no more than 70 to 80 cm.

Elk become aware of an approaching enemy mostly through the senses of smell and sound. Vision is relatively poor in this animal and its ability to identify an immobile man far away poorer than that of a reindeer. Before lying down elk usually turn leeward, make a semicircle or loop, and lie anywhere on an elevated site, sometimes behind a tree or with their head facing upwind. The approach of an enemy in such a position is noticed well in advance (Petri, 1930; Kaplanov, 1935; Semenov-Tyan-Shanskii, 1948; Kalnin'sh, 1950; and others). In the bed elk sleep or ruminate; they never sleep while standing.

Elk rarely attack man; usually only males in the period of rut or injured animals do so. An injured animal is extremely dangerous since it can easily kill a man by kicking with its forelegs (Buturlin, 1934).

Depending on activity, the body temperature of elk varies widely. Under great physical stress it may rise to 41°C; in winter it is usually 35.8 to 37.0°C, being somewhat lower at 34.0°C in young animals (Knorre, 1953).

Even moderately large groups of 12 to 18 elk are rare and such herds usually break up soon. In summer adult females move with

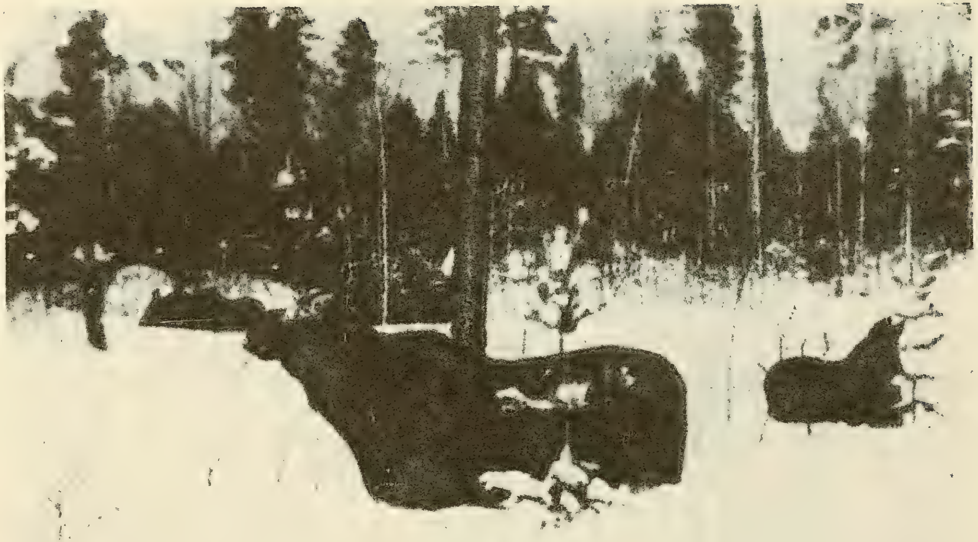


Fig. 86. Elk during winter foraging. Depth of snow cover 120 cm. Elk farm of the Pechora-Ilych preserve. March 1951. Photograph by E.P. Knorre.

calves, often including those of the previous year, while males and barren females live singly and rarely join together in mixed or single sex pairs and groups of up to three or four animals. At the end of rut some continue to live in pairs, and calves and often 1.5-year-olds join them. Sometimes even foreign adult elk join the group. Such a group may number from five to eight or even ten elk.

Some old males after rut live singly throughout winter while much younger ones band together in small groups to which barren females or 1.5-year-old males sometimes attach themselves. The latter, separated from their mothers, are often encountered in pairs. The herd instinct is more intense in winter than in summer, and in winters of heavy snowfalls than in winters of moderate snows. In Pechora-Ilych preserve the herding index from October through February (1934 to 1938) varied from 1.7 to 2.7 animals; in March, when the snow cover was highest, it rose to 3.7 (Teplov and Teplov, 1947). Herds break up in spring. Gregariousness is more pronounced in those parts of the range where population density is high.

Seasonal migrations and transgressions. Elk are significantly better adapted to living under conditions of a snowy winter than many other ungulates. They often winter in places abandoned by roe deer and even red deer. In regions with a mean maximum snow cover not more than 30 to 50 cm deep and a short period of heavy snow (central region of the European part of the USSR, much of Yakutia, and elsewhere), most elk winter in the same locality where they occur in summer, performing only minor transitions from one area to another. Elk lead a relatively settled life in the Baltic region and Belorussia even though the snow there is more (mean maximum snow cover not less than 50 cm deep; Rikhter, 1948). In Belovezh Forest elk wanderings were recorded in the past (Kartsov, 1903), which ceased after the population of ungulates in the forest decreased and the Pinsk marshes dried up.

The behavior of elk differs in places where the mean maximum snow cover in winter reaches 70 cm or more and the heavy snow period is fairly prolonged. In such localities elk concentrate in winter in the less snowy sections or move into other regions.

Seasonal migrations of elk in the northern parts of their range in regions of heavy snowfalls are quite extensive. Elk live here in taiga plains and wander in winter into less snowy regions, which are more convenient for wintering from the viewpoint of habitat (see section
274 "Habitat"), abundance of tree food, etc. (Arkhangel'sk district, Komi Autonomous Soviet Socialist Republic, and western Siberia). The length of migratory routes of elk during seasonal migrations in

these regions sometimes reaches 100 to 300 km (Kaplanov, 1935; Knorre, 1953; Nasimovich, 1955; Semenov, 1956; Shubin and Yazan, 1958; and others).

Mass seasonal migrations of elk are also distinct in some montane regions with a high snow cover where some mountains play a role in climatic boundaries. Elk migrate in winter into regions protected from snow by "mountain screens". Such types of migrations of elk have long been known in the Urals where snow is heavy on the western side and relatively lighter in regions east of the range divide. The animals move in autumn and early winter from west to east, from western Ural to Trans-Ural, and vice versa in spring. The southernmost point for which information is available about the existence of regular elk wanderings through the Urals is the southern extremity of the Ural-Tau mountain range (about 53° N lat.), while the northernmost point is the upper course of the Ilych (north of 63°). The distance between them exceeds 900 km. The territory from which elk migrate in winter through the mountain range to the east extends in the west from the watershed divide for roughly 100 km. However, the distance traversed by wandering elk, reckoned from end to end, reaches 200 km in some regions of the Urals. The density of migrations can be judged from the fact that in the mid-1940's from 4,000 to 6,000 elk migrated annually from the Perm region alone to winter "beyond the Urals" (Kuklin, 1946).

In several montane regions with a high snow cover elk move in winter into other sections (montane regions of the Kola Peninsula, Stanovoy range) or descend along the mountain slopes (the Altai, Sayans, and Barguzinsk ranges), wandering right down to the foothills in particularly snowy winters. The distance covered by elk wanderings may add up here to several scores of kilometers.

In montane regions in the southern Far East (Burein range, Sikhote-Alin, and others), during the first half of winter elk occur in large numbers at a higher level along mountain slopes than in summer, and descend only in February or March immediately after the snow becomes heavy (Vetlitsyn, 1894; Emel'yanov, 1927; Kaplanov, 1948; Abramov, 1949). The migration of elk in winter to higher altitudes in mountains is explained not so much by ecological factors as by the fact that hunting commences at that time of the year in the lower regions of the taiga. The presence of large numbers of men and dogs results in the migration of elk into deserted regions by climbing mountains where, in spite of some snow (40 to 60 cm) but not enough to impede their movement, the environs are quiet and safe (K.G. Abramov). Other reasons such as the absence in upper montane zones of wolves and competing species of ungulates could also be incentives for migrations (Nasimovich, 1955).

In many regions, in addition to wandering elk, some resident animals are seen. According to Krylov (1926), in the 1870's elk in the region of the Kolva River (Vishera basin), which had not crossed the Urals before mid-December, could not negotiate the range later because of high snow. Sighting such a helpless elk in February when the snow cover was high, often up to 140 cm, hunters bagged it without difficulty. Thus hunting acquired a selective importance and helped eliminate from the population animals inclined toward a more settled way of life (Nasimovich, 1955).

The seasonal wanderings of elk, like those of other ungulates, depend largely on population density; a small population can live year-round on local foods, which would prove inadequate for a larger group. During the 1910's in the upper reaches of the Un'ya and Shizhim (upper part of the Pechora basin), mass seasonal migrations of elk were recorded (Belousov, 1915), which ceased with a reduction in population. In 1934 the extensive (1,200,000 hectares) Pechora-Ilych preserve was organized, after which the elk population was gradually restored. Yet in the first few years of existence of
275 the preserve extensive migrations of elk never occurred. Only local migrations were observed, with elk congregating en masse in winter in river valleys and adjacent watershed areas covered by boreal forests, pine groves, and burned-over forest sections (Teplov and Teplov, 1947).

Mass seasonal migrations of elk from the Pechora-Ilych into other regions occurred for the first time in 1945 and have continued regularly since. Now (1958), part of the elk population winters in the preserve and part (evidently a minority) from regions adjoining the Ural mountains migrate eastward in winter through the mountain range. The majority of elk from the main territory of the preserve migrate in autumn southwest and southeast in the direction of the divides of the Pechora, Kama, and Vychegda, covering a few hundred kilometers.

The following figures provide a good idea of the magnitude of elk migrations in the Pechora basin: in the latter half of November, 1947, about 600 migrations of elk southwest for a distance of 150 km were recorded through the Ilych River, serving at that time as the northern boundary of the preserve. In December, through the southern and western boundaries of the preserve over a stretch of 200 km, 250 crossings of elk occurred beyond the limits of the preserve in a southwesterly direction. Within the preserve itself in that year no less than 600 animals wintered, representing new arrivals and local elk (Knorre, 1953). In autumn of 1955, 9 km from the farmhouse office of the preserve at Yaksha, no less than 1,000 elk moved through a section 6 km long (Shubin and Yazan, 1958).

The transit of elk toward the wintering site is usually gradual and continues for two months or more from October (sometimes, rarely, even from September) until early December, sometimes from November through December or even January inclusive. The commencement of mass migrations of elk to wintering sites often coincides with the first significant snowfalls, after which a permanent snow cover forms. At other times the initiation of migration coincides with the period when the snow cover on the summer range reaches 25 to 45 cm. Sometimes elk move out for wintering even before snows begin, immediately after the first significant cold snaps. Other elk remain in summer areas until the snow cover reaches 60 to 70 cm and the animals begin to experience considerable difficulty in moving around. In most cases they go through the period of rut in the same region in which they spent the summer.[267]

In autumn elk move singly, in pairs, or in small herds. They cover 10 to 15 km in a day, sometimes up to 30 km, and then remain for some days at a particular place (Dem'yanka basin; Kaplanov, 1935). In the Pechora basin the first to go are females with calves and yearlings, while adult males and females without calves mainly move out at the end of the migratory period (Shubin and Yazan, 1958).

Spring migrations occur over a very short period, mainly when snow thawing is maximum. From the Dem'yanka basin elk leave in spring in April; in years with frozen snow crust they move singly and in pairs after thaws commence (Kaplanov, 1935). In spring the first to leave are usually adult males and females without calves, and the last females are with calves (Malaya Sosva and the Pechora basin). In case movements have ceased during crusted snow formation, then migrations are particularly intense after the crust has cleared. In the spring of 1942, from April 29 through May 3, in an 80 km stretch between Nyagyn and Khangokurt, V.V. Raevskii counted 200 tracks of migratory elk moving north (Konda-Sosva preserve). In some regions part of the elk returned to their summer habitats only in June (Nasimovich, 1955).

Often the routes of elk migrations are extremely regular. The animals prefer to move along river valleys; in mountainous country they often select slightly longer routes, but with a less rugged topography. In the 1870's elk wandering in winter from the Kova River

---

[267] According to Abramov (1954) elk migrate during the course of rut from the upper courses of the Bikin.

beyond [east of] the Urals initially moved southeastward. At Berezovsk Kamen' their course turned steeply southward parallel to the
276 mountain range and then northward. Near Chuvamsk Kamen' they crossed the Vishera and again moved south parallel to the mountain range up to the valley of the Vels River, from whence they turned east across the divide (Krylov, 1926).

Long transgressions of elk, 100 to 200 km or more, into tundra and steppe have been recorded repeatedly. Usually they occur in the warm season of the year. With the approach of winter, the animals move away into forest regions or congregate along river valleys where woody vegetation is available. Since the early 1950's elk transgressions into open tundra around Nenetz have been a regular phenomenon. The animals arrive there in spring from the south (in the spring of 1957 about 20 groups of elk moving northward were counted on the Malozemelya tundra), and move in a reverse direction in autumn (Skrobov, 1958). Similar migrations of elk (in spring into tundra and in autumn into forest-tundra toward river valleys where there are genuine forests) have been observed from the latter half of the 1950's in the Taza Peninsula (Gromov and Rapoport, 1958).

During the last ten years elk transgressions into large towns have been reported, probably the result of high population density.

The colonization of elk in regions from where they had disappeared earlier for some reason or the other is discussed later (see "Enemies, Diseases, . . .").

Reproduction. Elk generally move in pairs during the period of rut and hence many researchers consider them monogamous animals (Buturlin, 1934; Kaplanov, 1935; Kuklin, 1946; Belyk, 1948; Kalnin'sh, 1950; Likhachev, 1955; and others). Monogamy of elk is not established, however. According to observations made in Pechora-Ilych preserve, rut in elk (1952 to 1953) lasts for only a few days (two to five, more often four or five) (E.P. Knorre).[268] As soon as one female exhibits disinterest in mating, the male often looks for another which has come into estrus later, thus covering quite a few females during the period of rut (Petri, 1930; Knorre, 1949; Peterson, 1955).

The presence of more males, often two and sometimes three, four or even six, near a single female in the period of heat has been observed time and again (Naryshkin, 1900; Petri, 1930; Kaplanov, 1935; V.V. Raevskii). In the Buzuluk pine forest and Pechora-Ilych preserve roughly 50% of the males in rut move with a single female;

---

[268] Swedish zoologists also point out that rut in elk continues for just a few days (Peterson, 1955).

in 30% of the cases two males move with the same female, in 10% more than two males, and in another 10% a lone male with several females (two to four) (Knorre, 1949). In Pechora-Ilych preserve one male in rut mated with seven females and all were impregnated. According to Knorre (1953) elk are polygamous. However, taking into consideration the fact that the tendency to polygamy is seen in this species only under certain conditions, such as high population density and marked predominance of females (because of selective shooting of males) or captive conditions, it would be more correct to regard elk as facultatively polygamous animals.

Combats are quite common among males over females, ending sometimes in the death of one or the other contestant (Teplov, 1948; Knorre, 1953; Nikul'tsev and Predtechenskii, 1957). Elk with body wounds and scars in the period of rut or immediately thereafter are quite common. Instances are known of several males attacking a bull that is accompanying a female (Kaplanov, 1935).

Some elk form pairs even before the commencement of rut—in the latter half of August. The male, moving usually behind the female, emits a sound generally described as a "moan," until the female is sexually aroused. This "moan" resembles more a hollow bellow, is far less audible than the call of a deer, and is usually heard for not more than 0.5 to 1.0 km, but over much longer distances under favorable conditions. Males "moan" at dawn and evening, rarely at night, and even more rarely during the day.

A sexually aroused male breaks the branches and tops of small trees with its antlers (such damaged trees can be seen even before the beginning of rut when elk clean their antlers), sometimes digs pits
277 with its hooves, and eats soil wetted with urine of females. Males exude a characteristic odor. Females, but more particularly males, abandon their usual caution in the period of estrus. Males become aggressive and permit the easy approach of man. The daily cycle of activity is disrupted. In males the hair becomes disheveled, the eyes bloodshot, and the neck thickens (Kaplanov, 1935). Males eat little at this time and lose up to 17% of their weight compared to that of the period before rut (Knorre, 1956). More aggressive males in the period of rut drive calves away from females and move singly, joining the female later. Yet in several regions during the period of rut calves and females with a single male are not an uncommon sight (Petri, 1930; Kaplanov, 1935; and Semenov-Tyan-Shanskii, 1948).

A male will mate with a receptive female several times in the course of a day. Mating is very brief, lasting only a few seconds (Knorre, 1953; Peterson, 1955).

The entire period of rut of elk, from moaning to the last mating, extends over 1.5 to 2.0 or more months. Mating is limited to much shorter periods—a month or slightly more (the majority of elk usually mate for 10 to 20 days) but some (usually younger individuals or those injured, etc.) mate much later. In Lapland preserve a newborn elk was found on July 4. The gestation period of elk is 225 to 237 days (Buzuluk Bor and Pechora-Ilych preserve; Knorre, 1953) and in some cases not less than 240 days (Perm zoo, Podososov, 1935; Serpukhov [Game]* Farm, Semenov-Tyan-Shanskii, 1948). Thus the female which calved so late had mated between November 5 and 20. In Quebec (Canada) a newborn calf was found on August 14, which means mating occurred not earlier than mid-December (Moisan, 1956).

In the southern and central parts of the range rut in elk is much shorter in duration than in the north. After a severe and snowy winter and an unfavorable summer (drought, etc.), rutting commences more gradually than in normal years (Abramov, 1949 and 1954). The duration of rut is undoubtedly influenced by the nature of autumn weather but authors do not agree on this fact. Rut in elk commences earlier and also usually terminates earlier in the southern and at some places (mainly within European USSR) in the central parts of the range. There elk mating, at least in some years, occurs even in the first ten days of September (southern Belorussia, Moscow and Saratov districts, Buzuluk Bor, Mordov preserve, Rybinsk reservoir, and Sikhote-Alin), and in some cases even at the end of August (Saratov district). Rut in elk in these regions terminates quite often at the end of September or early October and more rarely on October 10 to 15.

In the northern parts of the range and also in regions with relatively severe climate, prolonged winter, and late spring, mating usually commences not before the second decade in September, mass mating occurring from September 15 to 20 through October 5 to 10 (northern part of Scandinavian Peninsula, Karelia, Lapland, Pechora-Ilych and Konda-Sosva preserves, Dem'yanka River, Yakutia, northern Amur region, etc.). Rut in elk in these regions terminates by October 15 to 25 but some animals mate sometimes even later.[269] Much later periods of rut in regions with cold climate should be regarded as arising due to natural selection; with early rut and calving, mortality among the young if cold spells return or predators attack, especially bears (see "Enemies, Diseases, . . .") will be much higher than among those born at a much later period.

---

*Word omitted in Russian text—Sci. Ed.

[269] Many references to the period of rut in elk conflict with data by the same researcher on the time and birth of calves. The commencement of the period of rut is usually reckoned from the time of pairing, most often from the first instances of male moaning, and more rarely the first actual mating. Furthermore, these are not precisely recorded. Hence data on the period of estrus in elk should be handled with more caution and corrected as far as possible to accord with dates of the appearance of young.

278 It is highly probable that the prolonged season of rut in some parts of the range, and hence of calving, is also of adaptive value and caused by fluctuating climatic conditions in spring. With respect to the Kola Peninsula, where the period of rut in elk is highly prolonged and the periods of snow cover vary greatly, the above conclusion becomes self-explanatory. Periods of rut vary widely in different years. In Pechora-Ilych preserve mating of elk in 1952 occurred from September 23 through October 10 and in 1953 from September 12 through October 12 (E.P. Knorre).

With the exception of some individuals, probably those from late calving or those which are sickly and lag behind in growth, all elk are generally capable of mating in their second autumn. However, under natural conditions many females evidently mate only in the third autumn. Mating by males before their third or fourth year is quite rare since they cannot compete with older bulls. Most younger animals become sexually aroused at a much later period than older ones. In 1933 older elk in Dem'yanka River basin became aroused from September 22 through October 12, while younger elk displayed excitation from October 4 through 20 (Kaplanov, 1935).

At places where elk are hunted often calving usually takes place in a less accessible or dense and less frequented spot—dense thickets, in young plantations, sometimes along river banks, in marshes, islands, peninsulas, etc. In Lapland preserve elk calve everywhere: in marshes, alongside creeks, in forests, in burned-over sections, and even in montane tundra (up to 500 m). If snow is considerable in the period of calving, calves are born in thawed patches (Semenov-Tyan-Shanskii, 1948). Before calving and in the first few days after it, the female usually drives away yearlings which have remained close to their mother throughout that period (Lenberg: cited from Peterson, 1955).

Calving is earliest in the southern parts of the range and at some places also in the central region (European part of the USSR)—from the end of April to the commencement of May and through May 20 to 25 (more rarely right up to early June). In some years some females calve there from April 20 or even at the beginning of that month. In Moscow and Vladimir districts the majority of elk calve around May 1 (V.G. Heptner). In the Rybinsk reservoir region (Darwin preserve) calving of elk occurs from around May 10 but newborns were seen in 1951 even by April 20 (Kaletskaya, 1953). In the

Saratov district the first newborns were seen in 1946 on April 5 and 6 and in 1958 on April 1 and 4; the last calves were found mid-May (Martynov, 1959).

Calving of elk occurs in Pechora-Ilych preserve, Karelia, Yakutia, and western Siberia from around May 10 (in rare cases, earlier) through June 10. In Pechora-Ilych preserve in 1952 young were born from May 27 through 31 and in 1953 from May 11 through 20 (E.P. Knorre). In Lapland and Konda-Sosva preserves, and also in the northern parts of the Scandinavian Peninsula, the majority of births take place in the last ten days of May and the first half of June. In Lapland preserve two instances have been recorded of calving of elk at the end of June to early July, which should be regarded as a fairly rare phenomenon. At places where elk undergo considerable seasonal migrations, calves are usually born in summer residences; in the event of an extremely snowy and prolonged winter calving often occurs in wintering sites (Komi Autonomous Soviet Socialist Republic; G.G. Shubin).

The female elk usually gives birth to one or two calves. Two calves, rarely one, are characteristic of the Baltic region, central regions of the European part of the USSR, Novosibirsk district, the Pre-Baikal region, left bank of the lower Amur, Okhotsk coast, and Yakutia. One or two calves are equally common in Belorussia, Baltics,* Lapland preserve, Saratov district, Buzuluk Bor, Dem'yanka River basin, and evidently also in the central Urals. In an overwhelming majority of cases one calf and very rarely two are common in Trans-Baikal, Dusse-Alin, and Sikhote-Alin.

In Lapland preserve 25 females with calves were found from the end of May through August inclusive in different years; of these, 44% 279 had two calves and 56% only one (Semenov-Tyan-Shanskii, 1948). In Buzuluk Bor over a five-year period elk with calves were sighted 79 times: 42% had two calves each and 58% one each (Knorre, 1939). In one of the Saratov district forests, of 13 females with calves observed in 1947, six had two calves each and the rest one each. In Pechora-Ilych preserve from 1938 through 1946, 108 females with calves were observed; 47% had two calves each and 53% one each (Teplov, 1948).[270] Of the 25 pregnant elk caught in Novosibirsk district, 23 (92%) contained two embryos each and only two one each (Likhachev, 1955). Kaplanov (1948) during a three-year study in Sikhote-Alin detected 23 females with calves, all of whom had only one calf each; two calves were rare exceptions. Only 10 to 25% of American moose in different parts of the range produce two calves each and the rest one each (Peterson, 1955). In Sweden three embryos were detected in a lone elk (Lenberg; cited from Peterson, 1955). A single female with three calves is considered a great rarity among American moose (Peterson, 1955).

---

*Inconsistency in Russian text—Sci. Ed.

[270] According to Knorre (1953) elk of Pechora-Ilych preserve produce two calves more often than one.

Differential fertility among elk in different parts of the range is quite evident, but the reasons for this phenomenon are far from clear, particularly since accurate numerical data are inadequate and those which are available are not always comparable. Some researchers take into consideration encounters of elk with offspring only in the summer months and others throughout the year, which is less exact (see below), etc.

The proportion of single to twin calves largely depends on the population composition of elk; moreover, it varies widely in different years. In a given locality fully adult females often produce two calves, while younger females deliver only one. In the first few years of organization of Buzuluk Bor preserve, young elk predominated in the population. As a result, from 1933 to 1936 the percentage of two calves with a single female was only 10 to 31%, which rose to 45 to 57% from 1937 to 1940 (Knorre, 1949). In Pechora-Ilych preserve the average offspring per female in different years ranged from 1.2 to 2.0. A greater number of offspring were noticed after normal and relatively mild snowy winters and a smaller number after severely snowy winters[271] (Teplov, 1948).

Among twins, one may be a female and the other male (47%), both males (30%), or both females (23%). The second calf of the twin set often dies. In Buzuluk Bor, according to data over a seven-year period, twins in May averaged 57%, in May–June 52%, May–September 46%, and over a 12-month period only 40% (Knorre, 1949 and 1953).

Some elk remain barren. In the Primor'e region barrenness is rare (Abramov, 1954), while in other parts of the range it reaches 30 to 40% (Pechora basin) or more. Barrenness is generally more common if elk hunting commences before the conclusion of the period of rut (Skuncke, 1949), or in the event of a severe winter when the period of rut is prolonged beyond the normal period. Among American moose usually not more than 50% of animals older than two years fawn every year, the rest fawning in alternate years. In Newfoundland, Ontario province, and Alaska the number of barren

---

[271] Whether calves in this case died in the first few days after birth or whether females with twins aborted more often has not been indicated by the author.

280 Fig. 87. Newborn calf on the Chuna tundra. Lapland preserve. July 4, 1939. Photograph by O.I. Semenov-Tyan-Shanskii.

animals may reach 60 to 65% of the population (Peterson, 1955).

Growth, development, and molt. Observations on elk born in captivity confirm that within the first 10 to 15 minutes after birth they can stand on their legs but fall down immediately. The pelage and umbilical cord are wet on the first day. By the second day calves move better even though their legs are still gangly and sometimes uncoordinated. From the third day they move freely and on the fifth day it is difficult to catch them; by the tenth day, they are not inferior to their mothers in the use of their legs; and at the age of two weeks they are excellent swimmers (Knorre, 1953; and others). Under natural conditions calves remain in one place for at least a week. When the mother goes away to feed or runs away on sighting a man, the calves remain hidden in the grass or bushes; the mother makes no
280 attempt to protect her young from man (Kaplanov, 1935; Semenov-Tyan-Shanskii, 1948; Knorre, 1953).

Lactation continues for 3.5 to 4.0 months, i.e., roughly until the commencement of the period of estrus. Some females, those which have not gone into heat, continue to lactate in November–December or even later (Kaplanov, 1935; Knorre, 1953; Likhachev, 1955; Peterson, 1955). A barren female, killed in Pechora-Ilych preserve at the end of December, yielded 200 g milk. The calf with her weighed 43 kg more than any other in the preserve (E.P. Knorre). On the elk farm of Pechora-Ilych preserve one female yielded 150 to 200 liters milk during the period of lactation with a maximum of 2 or even 3 liters per day (June to early July)[272]; the daily yield was minimal at the commencement and termination of lactation. The fat content of milk in May–June was 8 to 10% and even up to 13% (Knorre, 1953; G.G. Shubin). Compared with cow's milk, milk of elk has 2.4 times more fat and ash, 5.0 times more proteins, but 1.6 times less lactose (Krott, 1956). Calves begin to eat green fodder around two weeks of age or a few days later (Podsosov, 1935; Shaposhnikov, 1951). In captivity calves attempt to nibble green leaves at the age of two or three days. Calves isolated from mothers at the age of 1.5 months and later fed on green fodder only, grew quite normally and were not inferior in growth to other fawns (E.P. Knorre).

A study of 56 calves raised in Pechora-Ilych preserve and Buzuluk Bor revealed that the weight of newborn female calves varies from 6 to 14 kg and of males 8 to 16 kg. Calves from paired litters generally did not weigh more than 10 kg. Calves weighing 6 to 9 kg were usually very weak and quite often died subsequently (Knorre,1949 and 1956; and others). Data on the weight of newborn calves from other parts of the range consist of occasional weighings (Lapland preserve, Serpukhov Game Farm, Dem'yanka River basin, and
281 Novosibirsk and Irkutsk districts) and do not differ from the foregoing. Data are not available on the weight of newborn calves of elk from northeastern Siberia where elk are largest in size in the USSR. In Scandinavia the normal weight of newborn calves is 10 to 16 kg and of twins sometimes 6 kg each (Skuncke, 1949).

Calves put on weight very rapidly and within six months their weight rises roughly tenfold, with an average of 120 to 130 kg, and in better developed animals 160 or even 206 kg. Weight increase in calves is relatively low in the first 1.0 to 1.5 months, when milk forms their food, as compared to the rise in the subsequent two months when large amounts of green fodder are consumed. In July the mean daily weight increase in Pechora and Buzuluk calves approaches 2 kg (Knorre, 1949 and 1956; and others). The mean daily weight increase in American calves in their first month is 450 to 900 g and in the second month 1,300 to 2,250 g (Trippensee, 1948).

From autumn weight increase slows down and by early winter when calves switch over completely to browse, it is even more retarded (southern parts of the range) or ceases altogether. In

---

[272] Improved methods of milking elk later raised the yield to 430 liters in a season (E.P. Knorre).

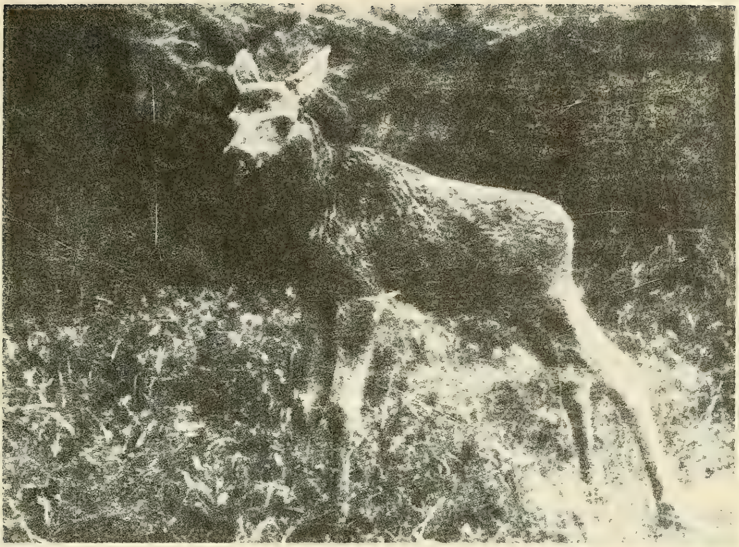


Fig. 88. Elk calf 25 to 30 days old. Southern part of Khabarovsk territory. July, 1957. Photograph by G.F. Bromlei.

Pechora-Ilych preserve the weight of calves remains unchanged from early winter right up to the cessation of the yarding period and spring molt, or even decreases in the case of a snowy and prolonged winter. Thus calves at the age of about one year weigh as much as at the age of six months and sometimes even less. Only in elk which have not undergone estrus and continue to lactate in winter, which rarely occurs, do calves, at least at the beginning of winter, put on weight even in the north (Knorre, 1956).

The height at withers of new-born calves is 70 to 90 cm, at the age of two months 105 to 110 cm, at four months 125 to 130 cm (Buturlin, 1934), in the winter of their first year 135 cm, and in the second year up to 155 cm. Adults stand 160 to 216 cm at the withers, more often around 175 cm (Knorre, 1953; and others). On the elk farm of Pechora-Ilych preserve calves usually do not grow up in height after October right up to spring, the winter–spring growth stabilization being even more distinctly manifested than that of weight (Knorre, 1956). Male calves at the Yakutia experimental station at the age of one month measured 107 cm at the withers and females 105 cm; at the age of three months, the corresponding heights were 120 and 117 cm, six months 139 and 132 cm, nine months 146 and 145 cm, and twelve months (females) 151 cm (Popov, 1939). The growth of these calves and their weight increase continued even in winter. The weight increase in elk older than a year is given in Table 3.

182 In their second summer elk continue to put on weight and under particularly favorable conditions (cool and rainy summer and few blood-sucking flies) attain 150 kg or more, so that their weight by 1.5 years of age has often doubled. Some elk weigh as much as 350 kg. The relative weight increase in elk is invariably maximum in their first year and the absolute weight increase, depending on weather conditions in summer, can be maximum in their first or second year. The weight increase slows down in the third year and the animal attains full physical stature in the fourth year. Later the weight of adult elk undergoes fairly regular seasonal changes, reaching 80 kg or more in amplitude and constituting up to 20 to 25% of the maximum weight of the animal in a given year. The maximum weight of elk is recorded at the end of August to early September and the minimum at the end of April to early May. During the period of rut males lose up to 17% of their former weight and in the subsequent winter three to five times less. In female elk weight reduction in the cold season of the year occurs very gradually; during the period of estrus, by November, they lose not more than 5% of their original weight (Knorre, 1956).

TABLE 3. BODY WEIGHT (kg) OF ELK IN THE EUROPEAN PART OF THE USSR AT DIFFERENT AGES (E.P AND E.K. KNORRE, 1956)

Sex	Newborn	0.5 years	1.5 years	2.5 years	3.5 years	4.5 years and older
Male	8–16	66–200	171–278	222–347	275–375	357–619
Female	6–14	69–140	175–331	227–345	275–360	347–406

Observations made in Sweden show that after the fourth or fifth year female elk do not put on weight, while males do not usually attain maximum weight before their tenth year (Skuncke, 1949).

Within a given age group weight variability is exceptionally high, as a result of which animals of different ages often weigh the same: males at the age of 1.5 to 3.5 years weighed in around 275 kg, while some 1.5-year-old females and animals aged 2.5 and 3.5 years weighed up to 300 kg (E.P. Knorre).

Data on the weight of elk in Siberia and the Far East are fragmentary but conform quite well within the range shown for the European part of the range. The maximum known weight of a Siberian elk (male) is 655 kg (Yenisey basin) and of a European elk

619 kg. One male in over a hundred elk killed between 1903 and 1912 in B. Petersburg province weighed 619 kg; the rest weighed no more than 477 kg each (Sablinskii, 1914). The weight of the largest bull in Buzuluk Bor was 563 kg and in Pechora-Ilych preserve roughly 500 kg; adult elk there usually range from 300 to 450 kg (Knorre, 1953 and 1956).

At places of intense hunting of elk maximum-sized animals are rarely sighted since most are taken in their first few years of life. Of over 100 elk killed in winter in southern Karelia not one weighed more than 311 kg (Knize, 1935). The maximum weight of a male caught in the Dem'yanka River basin was 422 kg and of a female, 370 kg (Kaplanov, 1935). The usual weight of elk in eastern Siberia is 320 to 400 kg and very rarely (males) up to 480 kg (Cherkasov, 1884).[273] Eleven elk caught in the Pri-Amur region weighed 260 to 320 kg (Abramov, 1954). Males caught at the end of September in 283 Sikhote-Alin weighed 400 kg each (Kaplanov, 1948) although Ussuri elk are considered the smallest in the USSR. Exact data are not available on the weight of the largest-sized elk of the USSR, i.e., from northeastern Siberia; the weight of males there in the bloom of their strength quite often reaches or even exceeds 600 kg.

In calves four to five months of age visible lumps have developed under the skin on the head by their very first autumn and antlers protrude from the end of April to early May through June inclusive, i.e., at the end of their first to early in their second year. Soft antlers harden only at the end of July or in August; their velvet gradually shrivels and is jettisoned by rubbing the antlers against small trees. These antlers measure 20 to 28 cm, sometimes up to 32 cm (Buturlin, 1934), and are often in the form of stubs without tines, bifurcate only in exceptionally rare cases. Young animals shed their antlers after older ones, usually only in February–March and sometimes even in April. The second antlers of elk form at the commencement of their third year and are bifurcate. Antlers with well-developed palmate portions usually form only in the fifth year. Later, given favorable conditions the weight of antlers increases, the palmate portion enlarges, and the number of tines increases. The weight of a pair of large antlers may reach 15 to 20 kg (Buturlin, 1934) or even more according to some authors.

New antlers commence growth in adult elk in April in the southern parts of the range and only in May in the north. Antlers attain full development at the end of June to the first half of July (quite often in June in the southern parts of the range). Thus their growth continues for 2.0 to 2.5 months. As long as the antlers are soft, they are very sensitive to impact and to insect bites. Hardening of antlers occurs in July; the tips of antlers remain soft most of the time in the form of round knobs and become sharp only later. By the end of August to early September velvet has been shed but this process occurs in Kola Peninsula only from the end of August through mid-September. At the commencement of the period of rut the antlers of adult elk are invariably free of velvet. In Sikhote-Alin young elk with velvet remnants have been sighted as late as September 17, while the antlers of old animals in some years are clean even by August 26 (Kaplanov, 1948).

---

[273] Kopylov (1950) gives the weight of 300 to 400 kg, exceptionally 600 kg, for the Irkutsk district.

Adult elk shed antlers from November (more rarely from the latter half of October) through December, sometimes extending up to early January.[274] In the Kola Peninsula and Yakutia elk shed antlers mostly in December. Three-year-old elk shed antlers in January–February. In old elk the palmate portions shrink, become lighter, and often even the number of tines is reduced. Under unfavorable conditions deterioration of antlers is seen even in animals no older than six to eight years (Knorre, 1953).

Elk are born with well-developed milk incisors and visible premolars. The formation of permanent incisors in Russian elk is completed roughly in their 18th month (Knorre, 1949). In American moose the first molar begins to erupt at the age of 10 to 14 weeks (that on the lower jaw somewhat earlier than on the upper) and functions fully at 4 to 6 months; the second molar begins to erupt at 6 to 8 months. At 13 to 16 months elk usually lose all the milk premolars and formation of molars ceases by 16 to 19 months (Peterson, 1955).

Young elk have rusty-colored wool, differing sharply from the grayish-brown of adult elk; their legs are not lighter in color than the trunk. Shedding of juvenile hair occurs from early August (slightly later in the north). By the middle or end of September young elk acquire the pelage of adult elk; at that time the legs become lighter in color and the trunk a dark brown (Knorre, 1953). In Lapland preserve elk molt in September, but young ones in juvenile coat have been sighted as a rarity even in November (Semenov-Tyan-Shanskii, 1948).

Data on the molt of adult elk under natural conditions are very scanty. One reason for this is the extreme similarity in color of

---

[274] Kopylov (1950) has evidently erred in stating that adult elk in the Irkutsk district do not shed antlers before February.

284 summer and winter coats, the former being only slightly darker than the winter dress. Elk molt once a year, in spring. By March the winter coat is perceptibly worn out and its luster lost. Guard hair begins to fall out at the end of March to early April and the underfur in the latter half of April. Molt commences from the head and legs and the last to molt is the back. Molt is most intense in May–June; however, females which have calved molt in June and the first half of July. In the northern parts of the range molt is delayed a week or two compared to more southerly parts. The first to molt are males and barren females and the last, females which have calved, and emaciated and sick animals. In Sikhote-Alin adult males molt early in July or even earlier, while females do so only toward August (Kaplanov, 1948). Normally fed males and females killed in the Dem'yanka River basin from July 16 to 20 had totally molted, while a female, still rearing her young and very emaciated, retained the remains of winter coat even on July 25 (Kaplanov, 1935).

The period of molt is difficult for elk, especially for the young. At that time body weight falls sharply or weight increase is arrested. Some young animals which have come through a severe winter lose up to 30 kg in weight during the spring molt (Knorre, 1949).

From the latter half of July to August elk sport a short lustrous summer coat; hair on the abdomen is very sparse. The skin is slightly thinner than in winter. In August the underfur begins to grow and guard hair elongates. During October,[275] or slightly earlier, elk sport a winter coat.

The strength of elk is at its peak from the age of 6 to 12 years. The prevalent view among Soviet zoologists is that elk live for no more than 20 years (Buturlin, 1934; Kalnin'sh, 1950; and others). However, a male elk tagged in Sweden as a calf and released was caught 20 years later and found to be in good health with antlers bearing 11 and 12 tines (Lenberg; cited from Peterson, 1955). In the Stockholm zoo a female elk calved at the age of 21 years but the calf did not survive (Skuncke, 1949). Judging from these data the potential longevity of elk is greater than 20 years and possibly exceeds 25 years as suggested by Cherkasov (1884). However, an overwhelming majority of the animals perish much earlier. In the elk population of Lapland preserve those older than 10 years constitute no more than 3% (Semenov-Tyan-Shanskii, 1948).

Enemies, diseases, parasites, mortality, competitors, and population dynamics. Among various predators attacking elk the most important are wolf and brown bear, the former mainly in the least snowy parts of the range and the latter in very snowy taiga.

---

[275] An adult elk caught in the Dem'yanka River basin on September 27 had a dark [summer] coat (Kaplanov, 1935).

A healthy adult elk is a difficult quarry for a wolf, the hunt posing a great risk to the predator: an elk kicking with the hooves of its forelegs can crush the head of the predator. Therefore, unless forced to, wolves do not attack elk. When other species of ungulates or cattle are available, elk are relatively rarely threatened by wolves. In 17 European, Siberian, and Far East preserves, several hundreds of remains of wild ungulates torn to pieces by wolves were recorded from 1945 to 1949; of these, only 5% were elk even though they were numerous (Kozlov, 1953). In Sikhote-Alin preserve, where other varieties of ungulates are also quite numerous, wolf attacks on elk have not been reported (Kaplanov, 1948; Abramov, 1954). Instances are known when females with calves in the summer approached within 100 m of a wolf's lair with litter, or lived from summer to spring in a region in which packs of wolves hunted, and suffered no attacks by these predators (Martynov, 1951; Peterson, 1955).

At the same time, when other food is scarce wolves can be very dangerous to elk and the resultant population losses sometimes very high. In 70 samples of wolf feces collected in Oka preserve, elk remains were seen in 77% (Borodin, 1940). In autumn–winter data 285 on the food of wolves in Darwin preserve (Rybinsk reservoir, 1948 to 1951; 90 feces), elk remains were found in 78% of samples. At this same place and in the same years, 11 young and 10 adult elk carcasses torn apart by wolves were found in summer; the corresponding figures in winter were 9 and 12. Thus, of the total number of elk killed by wolves, young animals accounted for almost 50% (Kaletskaya, 1953).[276] Wolves are responsible for considerable losses of elk in the Kalinin district (V.N. V'yunkov).

Young animals, which wolves attack mainly when they stray away from their mother, come first in the order of elk decimation; juveniles, just when they have taken to independent living, come next; and sickly and emaciated adults last (Buturlin, 1934; Murie, 1944). Wolves usually attack adult elk only in packs and avoid frontal attack. When wolves which have specialized in hunting elk later attack cattle or horses, they hold the prey by the groin and not the neck as commonly done (Kalinin district; D.P. Bengard). The damage to elk by wolves is higher in snowfree and least snowy periods of the year. Wolves find it difficult to overcome not only adult elk but even juveniles in soft and deep snow.

---

[276] In the national parks at Jasper and Banff (Canada) elk calves represented 100% of prey killed by wolves in summer, and just over 50% in winter (Cowan; cited from Peterson, 1955).

As a result of intense development of taiga regions in the Soviet Union in the last two decades, large forest areas have been felled and roads laid. Wolves have penetrated some of these regions of highly snowy winters, where formerly they were absent, and the damage inflicted on elk by these predators is steadily increasing. Instances are known of wolves which previously had never attacked elk later mastering the technique of hunting and killing them in large numbers (Perm district; Semenov-Tyan-Shanskii, 1948).

Elk suffer great damage from brown bear mainly in the highly snowy taiga regions, especially in spring when the predators emerge from their dens, while the snow cover is often deep. Deprived of other food sources, bear chase elk on pack ice. The chase sometimes covers several kilometers. In Lapland preserve the spring feces and stomachs of bear revealed elk remains in 35% of the samples; such finds were seven to nine times lower in summer and autumn. Of the 20 elk killed by bear in the Lapland preserve, 54% were adults, 25 to 33% animals in the second year of life, and 13 to 21% calves. Among the elk killed, one was pregnant with two calves and another in the process of calving (Nasimovich and Semenov-Tyan-Shanskii, 1951). In Pechora-Ilych preserve 10 deaths of elk caused by bear have been established. Of the dead, six were adults, one in the second year, and three calves (Teplov, 1953). Deaths of elk caused by bear have been recorded in several other regions of the country. According to Kaplanov (1935), in the event of an early spring, bears can destroy much of the calf crop of elk (Dem'yanka River basin). Evidently a high bear population could greatly affect the growth of an elk population. Instances of elk killing or injuring an attacking bear have also been described (Iokhel'son, 1898; Teplov, 1953; and others).

Other predators are not significant although some researchers hold that wolverine inflict as much or even greater damage on elk as bear (Teplov, 1948; Knorre, 1953). Young (up to one or two years) and pregnant females and injured or intensely emaciated elk suffer most from wolverine (Kozhanchikov, 1924; Teplov, 1948 and 1955). Among elk killed in Pechora-Ilych preserve by wolverine, four were under one year (one lame), two of the eight adults previously injured by poachers, and one chased a long time by a lynx before the wolverine attack. Three pregnant elk chased by wolverine aborted and the predator ate the fetuses. Most elk are caught by wolverine in February–April by an attack from ambush or by an active chase (Teplov, 1955; V.P. Teplov). In Lapland preserve not one instance of wolverine attack on elk has been observed; the remains of elk in wolverine feces are the result of scavenging (Nasimovich, 1948).

286 Probably in other parts of the range wolverine is also more often a scavenger than a true predator of elk.

The lynx is usually considered an enemy of elk (Cherkasov, 1884; Buturlin, 1934; Kaplanov, 1935; Belyk, 1948; and others) but actual data have not confirmed this assumption. In Sikhote-Alin and the Altai attacks of elk by lynx are not known (Kaplanov, 1948; Dul'keit, 1953), but such instances have been recorded in Pechora-Ilych preserve (Teplov, 1955). Analysis of tiger feces in Sikhote-Alin revealed elk remains (Kaplanov, 1948); elk constitute 10% of the victims of tiger in this region (G.F. Bromlei; Sludskii, 1953). No reliable reports of attack on elk by other predators are known.

Despite the endurance of elk in deep snow, in very snowy winters, especially if the animals are persecuted in that period, population decimation rises notably. After the snowy winter of 1894 to 1895 in the Kolyma basin elk were so severely emaciated by spring that they could barely stand on their legs and calves dying from hunger were found (Iokhel'son, 1898). A considerable number of elk died in Siberia during the extraordinarily snowy winter of 1913 to 1914 (Grum-Grzhimailo, 1914; and others). In Pechora-Ilych preserve, where the snow cover in some years reaches 110 to 120 cm or more at wintering sites, many elk are severely emaciated by spring. In particularly snowy winters death due to wolverine attacks increases, abortions are more frequent, newborns have a low body weight, are very weak, and soon die; ultimately the number of young in the population perceptible drops (Teplov and Teplov, 1947; Knorre, 1953 and 1956; Teplov, 1955; and others). After extremely snowy and prolonged winters, females calve in wintering sites where a large number of young evidently perish on their migration to the north (G.G. Shubin).

A prolonged spring with cold spells and snow, like autumn rains with frost and wind, is unfavorable for young elk. Population decimation is high in such years. In summer the most favorable conditions for the well-being of elk are cold and relatively rainy weather[277] and few blood-sucking flies. When the latter are excessive, some elk do not gain weight in that period (Knorre, 1953; and others).

Elk swim well but instances of their death in water are nevertheless not rare. In Pechora-Ilych preserve a total of 50 deaths of elk over a number of years have been recorded, of which 60% were due to drowning, mainly while the animals were traversing thin ice in autumn, 38% due to predators, and 2% due to other reasons. Adult animals drown most often since having broken through the ice they find it difficult to climb out of the hole. The maximum number of elk drown in years of prolonged obstruction by ice floes in the period of autumn–winter migrations (V.P. Teplov). In the southern Ural deaths have been recorded for elk attempting to swim through floating ice in the Beluya River (Kirikov, 1952) and animals caught in the high waters of the Ural River (Pashkov, 1958). When the Rybinsk reservoir was flooded in the spring of 1941, over 100 elk died because debris obstructed their passage (Turov and Kuznetsov, 1948). In Buzuluk Bor one elk drowned by falling into a pit in a peat bog (Teplov, 1948). Once a female elk swimming with small calves drowned (Peterson, 1955).

---

[277] In the Pri-Amur region an excessively dry summer or an excessively rainy one is unfavorable for elk since availability of food is lower (Abramov, 1949).

The diseases of elk have not been studied well. The maximum number of references are to Siberian ulcers in the Baltic region (Yurgenson, 1935), Mordov Autonomous Soviet Socialist Republic and western Siberia (Sludskii, 1954), and Yakutia (Belyk, 1948). In some regions Siberian ulcers raged through the elk population (Usually concurrent with an epizootic of Siberian ulcers among cattle) and a large number died in the eighteenth and nineteenth centuries in the Baltic region and in 1913 and 1914 in Yakutia. In the summer of 1950 in several regions of western Siberia carcasses of elk dead from Siberian ulcers were found.

287 Instances are also known of elk suffering from cattle plague, necrobacillosis, emphysematous carbuncle, foot-and-mouth disease, and scabies. Foot-and-mouth disease has been detected among elk in the Leningrad district. Emphysematous carbuncle has evidently occurred in Buzuluk Bor (Knorre, 1953; and others). In the Komi Autonomous Soviet Socialist Republic domesticated reindeer have suffered repeatedly from necrobacillosis but only three instances of elk attack have been recorded (G.G. Shubin). In Karelia blood parasites of family Piroplasmidae, causing hemosporidiasis, were isolated from the carcass of an elk (Chuzh and Bazhenov, 1951). The cause of elk mortality often remained undiagnosed in earlier years, for example in the Baltic region and in 1907 in the former Olonets province (Blagoveshchenskii, 1912).

On the elk farm of Pechora-Ilych preserve gastrointestinal diseases of nursing calves are common as a result of disorders in their natural feeding regime. Instances are known of the death of newborn calves due to colibacillosis. Calves suffer from inflammation of the lungs, almost invariably with fatal consequences (Knorre, 1953). American moose suffer from brucellosis (Corner and Connell, 1958), tuberculosis, various diseases of the respiratory tract and other organs, chronic leukoencephalitis, actinomycosis, arthritis, and malignant tumors. In captivity deaths from necrotic stomatitis have been established (caused by *Actinomyces necrophorus*) (Peterson, 1955; Ritcey and Edwards, 1958). A mass outbreak of rabies in Alberta (Canada) also affected elk (Ballantyne, 1958). For over 25 years a mysterious "moose sickness" has killed many moose in the USA and Canada. Its main symptoms are: loss of fear of man, lower mobility, uncertain movement, weakness, increased flabbiness, total or partial blindness, lack of response to approach, and loss of appetite. Eventually paralysis of the legs sets in and thereafter the animal dies. Many ticks have been noticed on affected animals. Suspicions about the viral and bacterial nature of the disease have not been confirmed (Peterson, 1955; Benson, 1957).

Among elk inhabiting the Palearctic, 38 species of parasitic worms (trematodes, cestodes, and nematodes) belonging to 16 families have been detected. Elk is an obligate host for several of these species (*Alcefilaria abramovi,*[278] *Nematodirella alcidis, Spiculopteragia alcis,* and *Verestrongylus alces*). Some species are known parasites of elk throughout its range in Eurasia (*Paramphistomum cervi, Taenia hydatigena* larvae, and others), while *A. abramovi* and *Parabronema skrjabini* are found only in eastern Siberia and *Fasciola hepatica* and *Parafasciolopsis fasciolaemorpha* only in Europe. Elk in zoos serve as hosts for various helminths (Rykovskii, 1957).

Among the most common elk helminths are *Trichocephalus* (in zoos) and *Parafasciolopsis* (under natural conditions). In elk infected with *Trichocephalus* the intensity of infection, according to available data, often reaches 5,000 or more parasites, leading to an extreme deterioration in the condition of the animals or even death (Rykovskii, 1957; Malyshev, 1958). Under conditions of intense infection by *P. fasciolaemorpha* (up to 19,000 parasites) normal liver functions are impaired and death may result. The intensity of infection of elk by *Paramphistomum cervi* is sometimes very severe, up to 9,000 parasites. The larvae of the latter two species of helminths grow in an aquatic medium. In arid years, when most small water holes dry up and elk are encountered around a few deep flood-plain water sources abounding in local intermediate hosts, the intensity of their infection by these helminths increases notably (Rykovskii, 1957).

Among helminths found in elk one should also include *Elaphostrongylus panticola, Dictyocaulus, Echinococcus, Nematodirus,* 288 *Ostertagia,* and *Moniezia.* Many species of elk helminths are also common to agricultural animals. Several helminths occurring extensively among American moose, for example *Wehrdikmansia cervipedes,* are unknown among Russian elk (Peterson, 1955; Ritcey and Edwards, 1958). Among the various reasons for the mortality of elk, the importance of helminth-borne diseases is not generally great. Under natural conditions a severe infection is seen in relatively rare cases; unless the animal is very thoroughly examined, helminths are generally not detected (Knorre, 1953; Abramov, 1954).

---

[278] Parasites in venous blood.

Several species of protozoans inhabit the rumen of elk (Dogel', 1934; and others). Instances are known of wild elk infestation with scab mite *Psoroptes equi* (Uhlrich; cited from Dubinin, 1955). In zoos the mange mite *Acarus siro* has been found on elk, transferred to them from other ungulates (Dubinin, 1955). Among Diptera the naso-pharyngeal gadfly *Cephenomyia uhlrichi* (represented in the Far East by the particular form *C. u. kaplanovi*) is prominent and evidently parasitizes elk throughout the range in Eurasia. This gadfly occurs en masse in July–August and sometimes part of September. The larvae parasitize the nasopharyngeal region. They were present in all elk caught in Sikhote-Alin in spring. Infestation occurs in June to early July (Pechora basin and Sikhote-Alin). When the larvae exceed 100, respiration and food intake become difficult, molt is delayed, and severe emaciation sets in, which in rare cases may cause death (mainly among yearlings). These larvae grow well in dry soil, as a result of which their most intense infestation of elk occurs in the year following a dry summer (Kaplanov, 1948; Grunin, 1957; Knorre, 1957). The larvae of the gadfly *Pharyngomia picta* infect many species of ungulates and also parasitize the nasopharyngeal passage in elk. The gadflies *Hypoderma alces* and *H. acteon* are known parasites of elk, mainly in the western (Baltic) and eastern (Trans-Baikal and Sikhote-Alin) parts of the range.

Horse flies (many species) greatly annoy elk and also act as vectors of Siberian ulcers. Their bites leave bleeding wounds on the hind legs of elk. Horse flies swarm en masse from mid-June through August inclusive (Kaplanov, 1935; Turov, 1953; and others). Other blood-sucking insects (mosquitoes, gnats, and biting midges) are of lesser importance than horse flies and gadflies, but the summer habitat-related dispersal of elk and their behavior greatly depend on the abundance and activity of pests since they affect feeding adversely (see "Daily Activity and Behavior").

On elk killed in the mountains of Sikhote-Alin innumerable blood-sucking flies of the family Hippoboscidae and ticks (mainly *Ixodes persulcatus*) were found. Due to their attacks the bodies of the animals were severely ulcerated (Kaplanov, 1948). The deer louse *Lipoptena cervi* parasitizes elk in several regions.

Many herbivorous animals are competitors of elk to various degrees. When prolific, muskrat can pose a serious problem (they eat aquatic vegetation) as also deer of the genus *Cervus*. In Belovezh Forest multiplication of red deer and a high population of other ungulates were considered responsible for the population reduction of elk there at the beginning of the twentieth century. In the 1880's and 1890's elk in the Forest had multiplied greatly. Then, with no significant intervention from man, their population rapidly dwindled from 775 in 1898 to 700 in 1901, 450 in 1902, 340 in 1904, 222 in 1907, and 58 in 1914. The living conditions for elk and other ungulates in that period in the Forest were less favorable since good tree and shrub foods were inadequate. Elk with signs of degeneration were seen—antlers without palmate portions, etc. (Kartsov, 1903; Vrublevski, 1912 and 1927; and others). White hare [arctic hare, *Lepus timidus*] is sometimes considered a serious competitor of elk (Teplov and Teplov, 1947). This is hardly correct since the hare strips willow at a much lower level than elk and feeds more on smaller shoots.

When the elk population is extremely high, irrespective of the
289 presence or absence of other species of ungulates, these animals per se can denude the winter food base. Under such conditions their population also begins to decrease as some elk evidently migrate, litter size drops, and sometimes mortality rises. In Oka preserve (24,000 hectares) the population density of elk, 20.2 per 1,000 hectares, had dropped by 1945 to 13.0 to 15.8 (Kozlov, 1954) and by 1951 even to 8.8. Only after the latter level was reached did some increase occur (11.5 in 1952 and 12.3 in 1953); in some western sections of the preserve it rose to a record level of 34.4 (L.P. Borodin). In Priok-Terras preserve (4,800 hectares) the average density from 1952 to 1955 was 20 to 25 elk per 1,000 hectares, which dropped to 16 or 17 in the next two years (Aleksandrova, 1957). In both of these preserves there were almost no serious ungulate competitors since sika deer (Oka preserve) and European bison (Priok-Terras preserve) were too few in number to be considered.

Similar phenomena have been observed in other parts of the elk range. Furthermore, depending on local conditions, i.e., dispersal of winter and summer habitats, state of food (especially of winter food), height of snow cover, presence of competing species and predators, protective cover, places of escape from enemies and blood-sucking flies, etc., the critical population level of elk may vary from 1 to 5 to 15 to 20 animals per 1,000 hectares.

The ability of preserves to retain elk revolves around some definite stages of forest "succession". For example, in the first few years after the destruction of forest (by fire, as a result of felling, or proliferation of pests), such an area can only serve as summer pasture for elk. Later, depending on the availability of shoots of aspen, birch, goat willow, and pine undergrowth, burned over and felled sections become excellent winter pastures of elk, especially if an old pine forest section lies nearby in which the animals can find shelters. This situation will obtain for 10 to 20 years (the lesser duration in the south and the longer in the north where forest grows more slowly), after which the forest begins to age for elk and not only the amount of accessible winter food reduces, but also its quality deteriorates.

In Arkhangel'sk district felled sections in the first ten years served only as summer pastures for elk and were not used in winter; they became excellent winter habitats for this species roughly from the twentieth year when protective conditions in them improved and tree food became abundant (Leble, 1953). After 40 years the ability of these areas to hold elk fell as food reduced. In Ontario (Canada) burned-over sections in relatively early stages of reforestation, i.e., up to 15 years, are considered most favorable for elk from the viewpoint of food availability. Their capacity increases up to 16 elk per 1,000 hectares. At the age of 16 to 30 years the capacity of a rejuvenating forest is assessed at 8 elk per 1,000 hectares, dropping to 4 at the age of 31 to 45 years, and to 1 after 45 years (Cringan, 1958). In highly snowy taiga regions the population dynamics of elk is determined not so much by the overall food resources of a given locality, as by the reserves of tree and shrub foods along rivers which constitute winter foods for elk (Knorre, 1953).

It is highly probable that intense changes in the northern boundaries of distribution of elk and in their population in several regions, observed time and again in the Soviet Union, were caused not only by the direct extinction and subsequent colonization of elk from adjoining regions where they were preserved, but also by changes in food availability of host areas due to forest fires (Pechora basin and western Siberia) and mass felling of forests (central regions of the European part of the USSR and central Volga basin). Climatic changes in this case were only secondary in importance,[279]
290 although they might have exerted some influence on this process

---

[279] The dispersal of elk northward is sometimes explained by the warming up of the climate in the Holarctic region (Peterson, 1955; and others), but if we remember that there should be an increased quantum of precipitation, including snow, as a result of the more intense circulation of warm moist air masses, the untenability of this assumption becomes evident.

(for example, promoting forest fires in drought years and preventing them in wet years, simultaneously hindering or promoting forest restoration). Thus Wrangel (1841, cited from 1948 ed., p. 280) in describing his 1822 summer journey into the lower course of the Kolyma points out for one of the left hand tributaries—the Filippovka River (entering the Kolyma below Bol'shoi and Malyi Anyui): "The Filippovka valley was formerly well known for many sokhati or Siberian elk. The great forest fire of 1770 drove them away, but later, as the forest rejuvenated they reappeared and multiplied so much within a short period that by 1812 rare was the hunter who did not bag half a dozen sokhati. Ten inhabitants of Panteleevka village caught 70 of them. One cannot state for certain the reasons, but after this event, sokhati again disappeared, and it is my understanding that this hunt was among the last of the lucky strikes. During our residence the appearance of sokhati in the Kolyma region was already considered a rarity and described as a bygone epoch in hunting. On the Omolon and south of it elk were still resident but in small numbers." Buturlin (1913), who visited the Kolyma River basin in 1905, remarks that elk were old inhabitants in its delta; they were absent there in the 1870's and 1880's but reappeared subsequently.

The composition of elk populations has been better studied than for most other wild ungulates. Among newborns the sex ratio varies highly, but on the average there is evidently some preponderance of males although the picture may be quite the opposite in some individual regions and years. In 50 elk litters from different regions of the country males represented 56% and females 44%, while in Buzuluk Bor (17 calves) males constituted only 30% but in Pechora-Ilych preserve (14 calves) 79% (Knorre, 1949). Later, a large amount of material from Pechora-Ilych preserve revealed that males constituted 62% and females 38% (V.P. Teplov). At places where elk are not killed the sex ratio in the adult population usually evens out to 1:1, but quite often favors females. This is evidently due to the higher mortality rate of males as a result of severe emaciation during rut, greater mobility and evidently less caution, and death resulting from fights over females.[280] In Lapland preserve among elk attacked by bear males constituted 67% and females 33% (Nasimovich and Semenov-Tyan-Shanskii, 1951). In Pechora-Ilych preserve among 19 elk which died for various reasons, males were somewhat more numerous (10) and in Buzuluk Bor numbered 8 among 12 dead (Teplov, 1948).

---

[280] Of 12 elk dead in Buzuluk Bor for various reasons, 5 were the result of injuries received by males in combats over females (Teplov, 1948).

In Lapland preserve among elk older than one year the sex ratio in the period June–December is close to 1:1 (97 females and 96 males; Semenov-Tyan-Shanskii, 1948). In Pechora-Ilych preserve the sex ratio of 2,330 elk older than one year was established in yards from 1938 to 1948; males comprised 52% and females 48% (Zharkov, 1952).[281] In Priok-Terras preserve winter counts from 1953 to 1955 showed that males among elk older than one year varied from 38 to 48% in different years and females were correspondingly 62 to 52% (Aleksandrova, 1957). In the Lithuanian Soviet Socialist Republic similar counts have shown that males averaged 42% and females 58% (V.A. Bergas). In ten regions of the European part of the USSR in the winter of 1943 to 1944 males averaged 42% (39 to 45%) and in the winter of 1945 to 1946, 43.8% (Danilov, 1949).

Selective hunting may strongly perturb the natural sex ratio. For example, at the beginning of the first decade in the hunting farm near present Krasnoe Selo (Leningrad district), there were only 60
291 males to 294 females. In other words, males represented only 17% of the total number of adult elk. As a result mating of females with juvenile males increased; such unions were evidently not always productive as off-spring were few (6.3%) and instances of degeneration observed time and again (Sablinskii, 1914).

The number of calves in a population is higher at the beginning of summer and lower in winter. Elk mortality is highest in the first one or two months of life (Knorre, 1953). By mid-winter calf mortality in the European part of the USSR has reached 50% (Danilov, 1949). In Pechora-Ilych preserve about 35% calves die by September–October and up to 60% in the first ten months (Teplov and Teplov, 1947). In Pechora-Ilych preserve calves in the population from June to August of different years have varied from 18 to 25%, on the average 21% (Teplov, 1948), and in yarding sites in winter from 7 to 23% (Zharkov, 1952). Young elk are few after winters of severe snows.

Elk counts in ten regions of the European part of the USSR revealed that the number of calves in the winter population of 1943 to 1944 varied from 25 to 33% (average 27%) and was 23.9% in the winter of 1945 to 1946 (Danilov, 1949). In the Tatar Autonomous Soviet Socialist Republic juveniles in winter in different years (1944 to 1950) constituted 26 to 29% (Aspisov, 1955) and in the Lithuanian Soviet Socialist Republic 17 to 22% (V.A. Bergas). In Lapland pre-

---

[281] During winter calculations, which provide the bulk of data for elk, the possibility should always be borne in mind that less experienced observers could mistake a number of males as females since at that time of year most do not bear antlers.

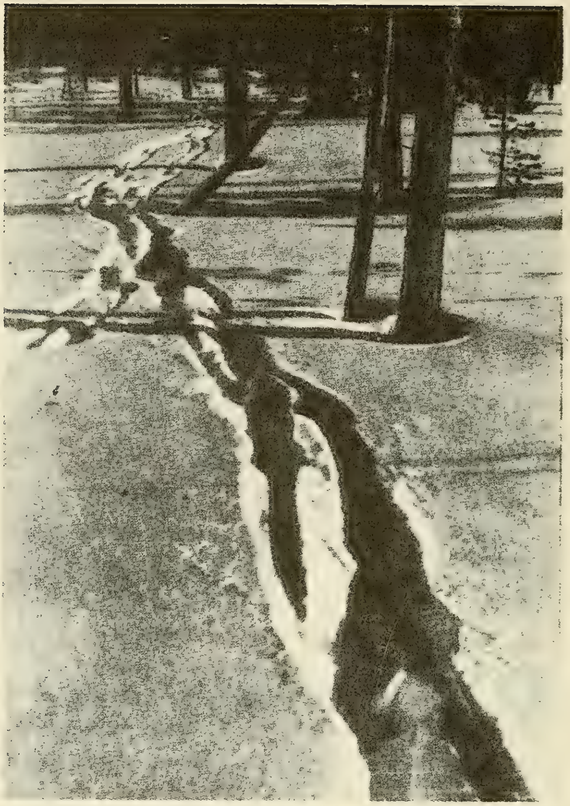


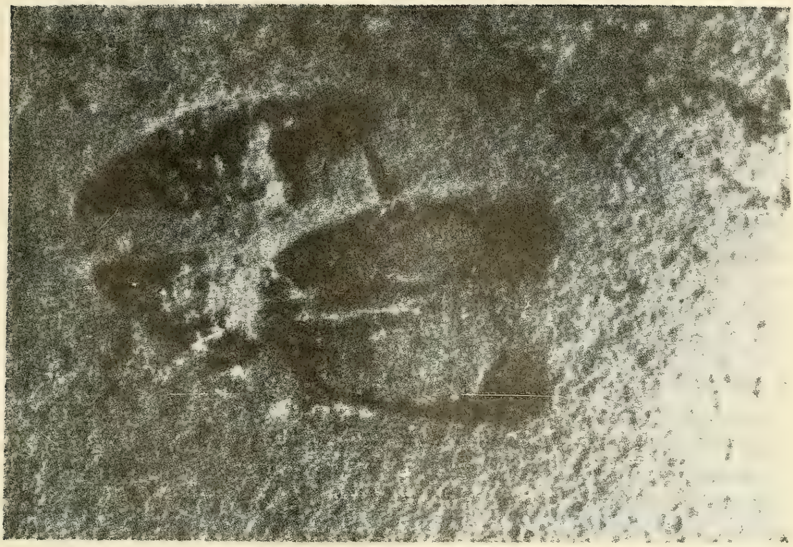
Fig. 89. Tracks of female elk with two calves (animals moving away from observer). Lapland preserve. March, 1951. Photograph by O.I. Semenov-Tyan-Shanskii.

serve the average for June to December was 21% (Semenov-Tyan-Shanskii, 1948).

Knorre (1953) considers 20% or more offspring in an elk population high, 15% average, and 10% or less low. In Canada this annual increase in elk population has on occasion exceeded 20% with an average of 16% (Peterson, 1955).

Field characteristics. Elk are not difficult to distinguish among other ungulates. Even young elk are readily distinguished from young of other deer by their long legs and absence of spots.

In winter, when males have no antlers (November to April), at a distance sex identification of elk from external appearance is difficult, since such characters as the usually smaller body size, lesser development of the dewlap and "beard," and slightly different pattern of coloration around the tail, etc. in females are not readily discerned. One must also take into consideration the group



292 Fig. 90. Track of elk in sand (without imprints of lateral digits). Lapland preserve. June, 1950. Photograph by O.I. Semenov-Tyan-Shanskii.

composition—adults versus calves. The urine stream in females falls between the imprints of the rear legs and in males in front of them. In females the hoof is prolonged with very narrow and sharp ends; in males it is usually larger, broader, and circular with blunt ends. The
292 tracks of males and females are therefore somewhat different but such differences are difficult to discern in soft snow.

The track of a moderate-sized male elk on the ground, excluding the imprints of lateral digits, is 152.5 mm long and 127.5 mm wide; in females the corresponding values are 140 and 101 mm (Buturlin, 1934). In large elk the track length can be as much as 175 mm. In yearling elk it is roughly 100 to 120 mm. The track of an average-sized male elk is invariably larger than that of a cow. Elk usually follow a beaten trail.

The direction of movement of elk on soft snow is best judged from the scatter of snow in front of the track and the greater compactness of the front wall of the "track impression"*, since the animal drags snow while shifting its legs (dragging in and dragging out of each track) and from other clues of movement (around bushes, toward trees, etc.).

Adult elk stand 160 to 216 cm, more often near 175 cm, at the

---

*Literally "glass [cup] of the track".

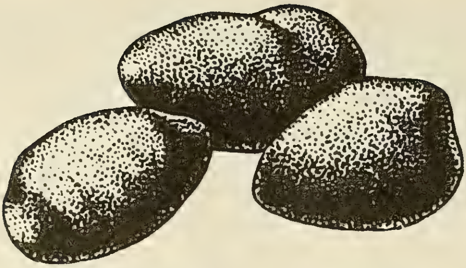


Fig. 91. Winter feces of elk (natural size). Moscow district. Sketch by T.L. Savranskaya.

withers. Calves in the first year are no more than 135 cm and in the second year 155 cm. The pace of an adult elk is 60 to 90 cm, which lengthens to 160 to 200 cm while trotting, and up to 3.5 m in jumping.

Elk lie on the snow without pawing it. The bed is kidney-shaped and 100 cm × 170 cm, 90 cm × 140 cm and 60 to 65 cm × 100 to 110 cm for males, females, and calves respectively. The depth of the bed into the snow surface may be 30 to 40 cm (Semenov-Tyan-Shanskii, 1948). Since elk sometimes stand only to lie down again a short distance later, the number of beds is often more than the number of elk in a group.

Winter and summer feces are in the form of oval pellets (4.0 to 5.0 cm × 1.5 to 2.0 cm; those of calves are not longer than 2.5 cm). In winter they are much firmer, with remnants of chewed trees visible in them; in summer they have an oily sheen, are black, soft, cohesive, and sometimes bear traces of semidigested grass. Widely recurring 293 statements in literature that female elk feces are invariably in the form of long pellets and those of males rounded are totally false (Knorre, 1953). In transitional seasons, especially spring, elk feces are often of a semifluid consistency, resembling those of bovines.

In summer pastures elk often nibble tops of tall plants (willow herb [=fireweed] and others); at places of feeding in the water, bits of *Nuphar* and water lily rootstocks, their leaves, etc. are often seen floating. Elk scrape tree bark with their incisors, leaving behind a chisel-shaped groove, or tear long strips by gripping the edge with the lower incisors and moving away from the tree. Sometimes bark is stripped to a height of 100 to 350 cm from the ground. Adult elk tear off the shoots of trees (first breaking them) most often at a height of 250 to 270 cm above the ground.

In rubbing the velvet off their antlers, and later right up to the moment antlers are shed, elk often use them to break young (up to 8 to 10 cm diameter) trees and twist and reduce them to splinters. In

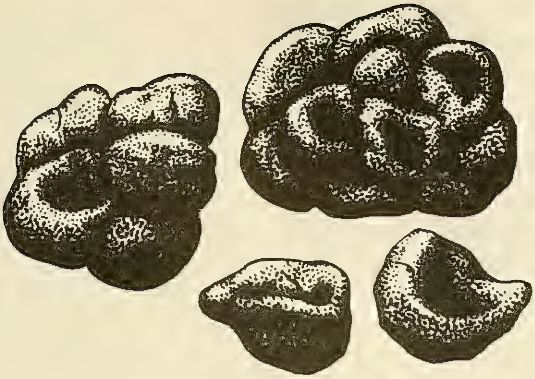


Fig. 92. Summer feces of elk (natural size). Moscow district. Sketch by T.L. Savranskaya.

addition they often maul and uproot bushes. Males in rut dig pits with the hooves of their forelegs to depths of 25 to 30 cm and up to 80 to 120 cm wide. The urine of the male in these places is highly pungent.

The voice of elk is most often heard in the period of rut when males moan (see "Reproduction" above) and females (often during mating) emit a sound similar to a snore or neigh. Calves emit a very soft moo.

Economic Importance

Among elk products, the meat is of utmost value. Its quality is superior at the end of summer to early autumn when a single elk can yield 30 kg of internal and subcutaneous fat (Kaplanov, 1948). After rut male elk lose up to 17% of their former weight (in the period of rut their meat is less edible) and later recover only slightly before the onset of winter. Females remain well-fed up to December through early January; barren females retain their weight slightly longer. Elk weight is lowest at the end of winter and in spring.

The body weight of an adult elk is most often 300 to 400 kg (for details, see section "Growth, Development, and Molt," and Table 3 above) but at places where elk are hunted intensely their weight averages a little over 200 kg. In autumn the meat yield varies from 60.0 to 62.5% (Buturlin, 1934; Knorre, 1939; Popov, 1939) to 64 to 65% of body weight; in barren females it possibly goes up to 70%[282] (Likhachev, 1955). At the end of winter the meat yield is much less since some elk during the period of estrus and in the following winter lose up to 80 kg (Knorre, 1953). The maximum meat yield of Pechora elk is 300 kg (E.P. Knorre).

---

[282] The meat yield of 69.5 to 75.0% quoted by Kaplan (1948) for Ussuri elk is an exaggeration.

Taking the weight of a European elk without antlers as 100%, the head (without antlers) constitutes 6.25% of total weight, fresh hide with lower parts of legs 10.75%, stomach and intestines (with contents) 17.0%, and carcass with liver, heart, and kidneys 62.5% (including blood, which accounts for 3.5%) (Buturlin, 1934). In
294 Yakutia it was established that the head weight without antlers constitutes 7.15% of total weight, fresh hide 11.75%, stomach and intestines 18.25%, and carcass 60.1% (Popov, 1939). Elk fat is of a greater fluid consistency than that of cows and has a good flavor. When animals are raised in captivity, their milk can also be used (see "Growth, Development, and Molt"). It is high in fat content and has a taste similar to the cream of cow's milk but without a salty-astringent aftertaste. The maximum milk yield in a season is 430 liters per elk but fat content corresponds to 1,290 liters of milk from local cows. One liter of elk milk can yield 110 g butter (E.P. Knorre).

In some regions local people also consume the blood of elk. The cecum is stuffed with congealed blood admixed with bits of meat and fat and sausages made from it (Amur and Sikhote-Alin; Abramov, 1954).

The thick strong hide is converted into high-quality chamois. Local people also used it in the recent past for making fur coats (with the fur outside; heavier than that of goat and deer), dresses, parkas (with fur inside), caps, winter footwear, mittens, etc. Elk hides are often used as bedding even today. Belts, straps, harnesses, and knitting bags are other products made from hides. The skin of the legs is stitched or glued to skis and used for soles of high boots. In summer flaws reduce the value of hides. The hair is utilized in mattress stuffing and furniture padding. Elk chamois is better than deer chamois in quality and in the eighteenth and nineteenth centuries was converted into breeches and other garments for battalions.

Antlers are used as trophies, in making knife handles, etc. In the past a medicinal meat-jelly was made from the horns and considered curative for tuberculosis (Turkin and Satunin, 1902 and Solov'ev, 1922). A good quality glue can be obtained from hooves and tendons are used as thread (Buturlin, 1934).

In the early 1920's about 70,000 elk were caught annually (Solov'ev, 1922). A much higher figure has been quoted for the end of the nineteenth century (Turkin and Satunin, 1902), but such figures are purely speculative. In the eighteenth and early nineteenth centuries elk as an object of hunting was evidently much more important and the well-being of local peoples at many places depended on the success of the hunt. In the seventeenth century, and probably even later, in the Sosva basin an elk cult developed among the local populace (Bakhrushin, 1935). According to data recorded in 1926 and 1927 for the pri-polar north of the USSR (data for Yakutia destroyed), 5,564 elk were caught in 1925 in regions of the Far North. The total catch of elk in the country in the early 1930's was placed by Buturlin (1934) at 10,000 which, according to him, exceeded the herd growth at many places.

In the hunting season of 1960 to 1961 in the Soviet Federal Socialist Republic licenses were issued for killing 18,000 elk (N.V. Eliseev). Actually, throughout the USSR no less than 35,000 elk are caught nowadays, but even with this number elk reserves are not thoroughly exploited (see "Population"). In many regions licensed hunting of elk should be increased, but poachers simultaneously discouraged. The permissible norm of hunting should be 15% of the total population (Knorre, 1953). Permission should be granted to hunt not only males but also females, but males should predominate roughly 2:1. When males are hunted in a higher ratio, the number of barren females increases notably.

Hunting elk at the end of summer (August 15 to September 15) is futile since the meat goes bad quickly at that time of year. Hunting elk in the period of rut is likewise foolish since the meat of males at that time is less edible; furthermore, hunting frightens the animals and barrenness subsequently increases (Peterson, 1955; and others). The best hunting period is from November 1 to December 1 (depending on the period of termination of rut and allowing two to three weeks thereafter for males to recoup somewhat, for a total duration of not more than 1.0 to 1.5 months).

At present the greatest numbers of elk are caught with the help of
295 dogs. Hunting with dogs is generally done in autumn and early winter on rough trails when the snow is still sparse. The hunter releases a laika dog (sometimes two or three) on the fresh tracks of an elk, the dog stalks the animal, and the hunter's approach to the quarry is thereby simplified. This type of hunting is practiced extensively throughout Siberia and the Far East. Sometimes the dog is kept leashed and the hunter moves along with it (Karelia, Irkutsk district, Pri-Amur, and others). During this maneuver the dog should lead the hunter to the elk without raising its voice; the hunter's job is thus doubly simplified.

In autumn and early spring, when the snow is not deep (up to 20 to 30 cm), especially during a fresh snowfall, elk are hunted on foot rather than on skis. In the past hunters rode on sledges (when the animals were less frightened) or on horseback (the Sayans) but these methods have now been mostly discarded. On skis hunters are relatively poorly hidden from elk since skis make considerable noise. Most elk in the European part of the USSR are hunted from places of concealment and by chasing (for which purpose a few hunters band together). This type of hunting is practiced in Siberia also.

Elk are also caught by organizing drives; sometimes flags are used but not all elk are frightened by them. In Siberia and Komi Autonomous Soviet Socialist Republic during autumn elk are often killed by shooting them in the course of their seasonal migrations.

Most other methods of catching elk are either banned or have been discarded. Among such methods are catching elk by driving the animals into an enclosure made on deep snow and surface crust. In the pre-Revolutionary period and the first few years after the Great October Revolution this method prevailed. Nowadays it is employed exclusively by poachers, mainly in the least supervised parts of the elk range. Chasing an elk is possible only when the snow is very high (a meter or more) but even then two or three men on skis often have to chase an animal for several days in relays before coming within firing range. If there is an ice crust on deep snow, hunting is greatly facilitated and often ends quickly; on crusted snow laika dogs are sometimes used to help arrest elk movement. At the end of winter elk become greatly emaciated and their meat dry and devoid of fat. Sometimes animals which elude the chase become overheated and later die.

There is no hunting of elk in the summer season. Formerly, elk at that time of year were often caught on water (sought by elk to escape blood-sucking flies and to feed on aquatic vegetation). Either an ambush was set up or a stealthy approach made from the bank or a boat. Elk are also hunted at salt licks (Sikhote-Alin) with the aid of dogs, but in summer even an experienced dog finds it difficult to restrain an elk. Autumn hunting from rafts, practiced mainly by privileged hunters in pre-Revolution Russia, has been discontinued. Hunting with a birch tube ("decoying") in the period of estrus, the hunter imitating the voice of a cow to lure a male, is also on the wane. This type of hunting ("hunting the moan") is largely a form of pure sport, since the meat of males at that time is hardly suitable for human consumption.

In pre-Revolutionary Russia various methods of trapping elk were widely employed, mainly by setting up long (up to 10 to 15 km) fences with exits in them where pits were dug, crossbows held at the ready, "runners" set (a log with a knife embedded in it to rip the animal's underbelly), and large traps laid. Fences were constructed at places elk passed through during seasonal migrations. A large number of elk falling into pits died for nothing since the pits were not supervised properly (the Urals, western Siberia, Yenisey basin, Trans-Baikal and Sikhote-Alin). Crossbows were also used at salt licks, on tracks, etc. This type of elk hunting was brutal and generally dangerous, and hence has been banned. Nevertheless poachers practice it even now, not only in Siberia but also in the European part of the USSR. Usually metallic snares and sometimes small guide fences are set up (Komi Autonomous Soviet Socialist Republic; O.I. Semenov-Tyan-Shanskii).

296 Experience gained in Pechora-Ilych preserve has shown that fences can be successfully used for catching elk in small enclosures. Part of the elk corraled are killed and part set free. The maximum number are trapped in such enclosures during migrations (Shubin and Yazan, 1958).

When the elk population is high, saplings and bushes in the forest and forest nurseries incur great damage.[283] In the European part of the USSR and also Scandinavia young pines (more often not older than 20 years) are damaged most. In the southern parts of the range many valuable species such as oak are also damaged by an excessive elk population, but only at places where pine are absent or few. Damage by elk to aspen, willow, mountain ash, alder, birch, juniper, etc. is of less significance to the forest economy since these species are less valuable. In the European part of the USSR the zone in which pine are severely damaged by elk extends from the Baltic region and the upper course of the Dnieper to the Ural River. Damage is maximum at places where a single elk has for itself an average of less than seven hectares of young pine forests (Dinesman, 1957). The critical form of damage is breaking of tree tops. Observations in Sweden have revealed that when the elk population density is extremely high (up to 30 animals per 1,000 hectares), up to 80% of the pine forest is damaged and 10 to 50% of the trees perish. Damage is maximum at places where deciduous species are intermixed with pine forests and higher in less dense forests (Westman, 1958).

Various methods have been implemented to protect valuable forests from elk: planting less valuable species along forest roads, feeding elk hay and cut aspen (in most regions elk consume hay poorly), fencing individual forest sections, applying oily substances to trunks to repel the animal, wrapping trunks with nylon, etc. (Westman, 1957; Dinesman, 1957; and others). None of these meas-

---

[283] Also see section "Population".

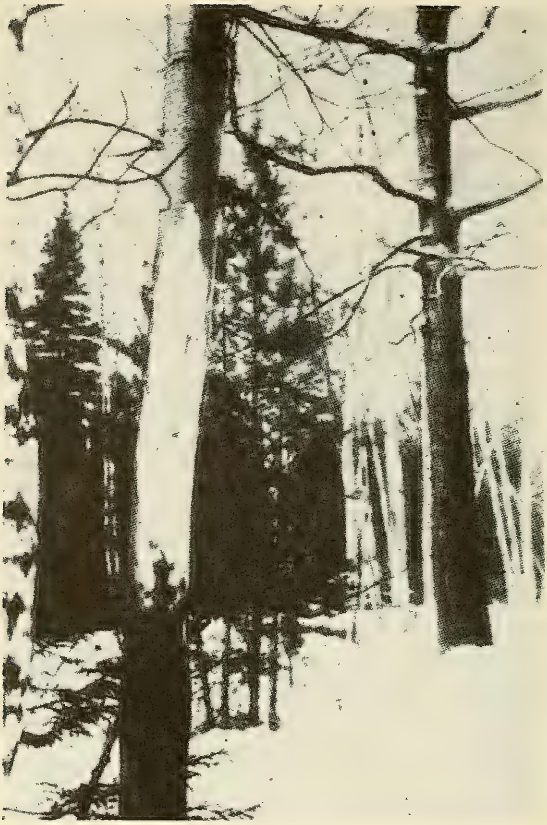


Fig. 93. Aspen with bark peeled by elk. Moscow district, 1949. Photograph by A.G. Bannikov.

ures attain the objective. They are either too costly or insufficiently effective. The only rational measure is the regulation of elk and a more intense utilization of their stocks.

Elk rarely invade cultivated fields; at places, however, elk in spring have damaged winter crops, oats, and melon fields (Voronezh district).

In the past various deformities in cattle calves were often ascribed to the mating of cows with elk.[284] This is completely impossible since these animals belong to different families.

297 Their large size, great strength, ability to easily negotiate areas cluttered with windfallen trees, hummocky or swampy areas, and high snow cover prompted people long ago to attempt domestica-

---

[284] This possibility was endorsed quite recently by Manteifel' (1934).

tion of elk. Domestication was facilitated by the relatively easy feeding of newborns, their tameness, and the abundance of winter food for elk. Later, their early maturation also became known; this, like their fertility, is better than that of domesticated cattle. Efforts to tame elk and harness them in the Soviet Union are known from the eighteenth century.[285] Right up to the end of the 1920's, however, such attempts continued to be random although essayed several times.[286] Attempts to tame elk were better organized in Berezinsk reserve area (Belorussia), Yakutia experimental station, Serpukhov farm, and Buzuluk Bor.[287] But this work has been carried out comprehensively and along proper lines only in Pechora-Ilych preserve where, in the early 1940's, an experimental elk farm was organized under the guidance of E.P. Knorre, formerly engaged in the domestication of elk in Buzuluk Bor. Elk reproduced well in the experimental farm. Several dozens have been raised and many tamed and used as pack, transport, and draft animals. A test run in harnessing elk was successfully conducted in winter over a distance of 240 km; during the test run they were fed branches and potatoes (G.G. Shubin).

Elk work best at a slow pace. Their most promising use is as pack animals and partly as transport animals in forests without roads for hunters, search parties, etc., especially at places where there are no lichens and the maintenance of reindeer is unprofitable. Elk are more successfully used in autumn and the first half of winter. Castrated
298 males (bulls in rut are dangerous) are most convenient for this purpose. These animals are incapable of working in the heat of summer. In the latter half of winter they become highly emaciated and less suitable for movement in thick snow cover. Elk also cannot be gainfully employed in spring when molt occurs. Thus the total duration of the effective utility of elk is evidently limited to less than 40 to 50% of the year.

The packload of yearling elk is up to 50 kg and on sledges up to 100 kg; corresponding values in the second year are 75 and 200 kg, and in the third year 100 and 300 kg, respectively. The daily run of yearlings should be restricted to around 10 km, in the second year to 20 km, and in the third year to 30 km (Knorre, 1953). The maximum

---

[285] Skalon and Khoroshikh (1958) think that the domestication of elk and their use as transport animals was in vogue even from the Neolithic period and was particularly well developed in the Iron Age, declining only later. This supposition is not supported by adequate data.

[286] Buturlin (1934) lists several such studies.

[287] Experiments were also conducted in Kostroma reserve zone, Tyumen, Novosibirsk zoo, and in Sikhote-Alin preserve.

297 Fig. 94. Elk as pack animals. Pechora-Ilych preserve. October, 1952. Photograph by O.I. Semenov-Tyan-Shanskii.

packloads are 135 kg and on sledges 500 kg (Popov, 1939) or even considerably more (E.P. Knorre). If trained from an early age, elk can be made to move quickly (E.P. Knorre).

Recently elk raised in Pechora-Ilych preserve were set free in an experiment throughout the summer. By autumn of 1958, 19 of the 22 elk released returned to the pen (the rest possibly died or were caught by poachers). Elk of the second and third generation raised in captiv-

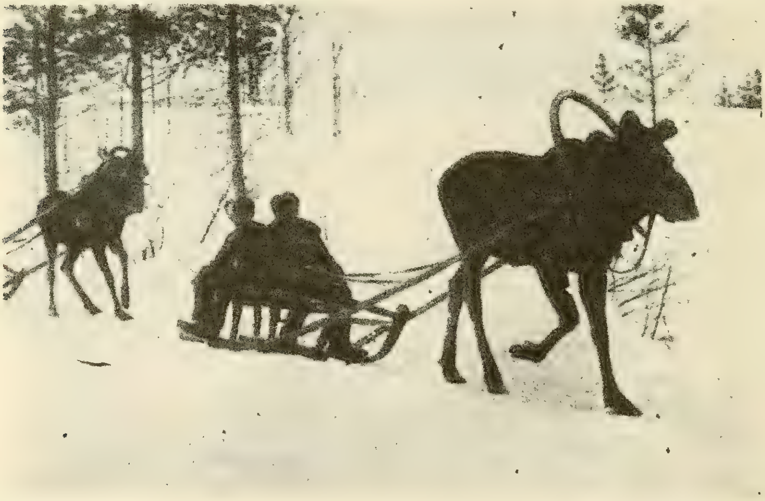


Fig. 95. Elk harnessed to a sledge. Pechora-Ilych preserve. December, 1953. Photograph by O.I. Semenov-Tyan-Shanskii.

ity were far easier to train than the first generation (E.P. Knorre). It would be premature to draw decisive conclusions just now on the profitability of raising elk. But it is quite clear that farms designed for selective catching of elk during their migrations should be self-supporting.

Elk remain year-round in many preserves. Some play a prominent role in restoring the elk population (Pechora-Ilych, Konda-Sosva, Altai, the Sayan, Sikhote-Alin, Oka, and others).

Within the Soviet Union experiments to reacclimatize elk have evidently only been conducted in Belovezh Forest where a nursery was set up and 10 elk from it set free in 1938 and 1939. By 1946, of these elk only three had survived (Sablina, 1955). It would probably be more useful to acclimatize elk in Kamchatka (Buturlin, 1934) where they would not encounter other competing species of ungulates. Serious attention should be given to the reacclimatization of elk in the western and central parts of Altai where they were exterminated in the nineteenth century. It would obviously be less useful to release elk in the northern Caucasus (Buturlin, 1934). (A.N.)

GENUS OF REINDEER*

299 Genus *Rangifer* H. Smith, 1827

1775. *Rangifer*. Frisch. *Natur.-Syst. d. vierfüs. Thiere*, p. 3. The name does not meet nomenclatural requirements.

1827. *Rangifer*. H. Smith. Griffith's *Cuvier Animal Kingdom. Mamm. Syn.*, p. 304. According to a resolution of the International Committee on Nomenclature (resolution No. 91), this should be used as the generic name. *Cervus tarandus* Linn.

1827. *Tarandus*. Billberg. *Syn. Faunae Scand.*, vol. 1, p. 22. *Tarandus lapponum* Billberg=*Cervus tarandus* Linn.

1845. *Achlis*. Reichenbach. *Naturgesch. Säugeth.*, vol. 3, p. 12. Substitute for *Tarandus* Billberg. (V.H.)

Rangifer are telometacarpal deer of moderate size, relatively slender build, with a fairly long trunk and neck and relatively short legs. Head proportionate in size. Tail short.

Entire metapodial region massive. Hooves of middle digits large, broad, and blunt. Hooves of lateral digits quite large and set low.

In general proportions the skull corresponds to that of red deer (*Cervus*) or is only slightly more elongated. Overall length of skull over twice that of malar width. Facial part of skull relatively high in region of commencement of nasals. Distance from front tooth to anterior end of premaxilla more than length of upper tooth row. Premaxilla of moderate length but longer than upper tooth row. Anterior end of premaxilla with a small pit. Nasal processes of premaxillae reach nasals. Nasal opening of normal dimensions, its length not exceeding that of the nasals. Nasals not shortened and longer than upper tooth row. Orbits tubular, project laterally. Lacrimals relatively narrow and elongated. Preorbital depression on lacrimal long and distinct but not deep or sharp in outline. Ethmoid pit large. Antler pedicels of frontals set upwards. Rear of vomer high and divides choanae into two separate portions. Tympanic bulla relatively small and auditory tube long. Lower jaw elongated and symphysis roughly equal to length of lower tooth row.

---

*Literally, "northern deer"—Sci. Ed.

Upper canines present and well developed in males, but very small in females. Upper molars relatively small, width less than height, and size of premolars hardly differs from that of molars. Lower tooth row weaker than upper and molars smaller than premolars. All molars with relatively low crowns. Lower incisors and canines relatively small, fairly identical, equal in size, and form a fairly even row. Dental formula:

$$i\,\frac{0}{3},\ c\,\frac{1}{1},\ pm\,\frac{3}{3},\quad m\,\frac{3}{3} = 34.$$

Antlers present in both males and females (only instance in the family). Antlers large and complex with a long main beam which runs upward and backward and then upward and forward. At the end of the antler lies a small flat vertical palmate portion with short tines set partly backward and partly upward, or else no distinctly developed palmate portions and only some small tines set backward; lower tine usually set not below the forward turn of the main beam (on the "elbow"). Brow and bez tines present (latter sometimes absent); they are large, set forward, and usually, at least on one side, form a fairly vertical palmate portion with small tines set forward. Middle tine and others jutting forward from beam absent. Antlers
300 quite asymmetrical; one of the first two tines may be absent, one of the pairs may have a palmate portion and the other not, the palmate portions may differ in size, etc. Antler beam and tines flattened and palmate portions on beam and tines flat. Invariably, antler surface completely smooth, as though polished. Antler color light brown or whitish.

Ears relatively short and fairly rounded. Muzzle densely covered with hair, fairly thick, but not enlarged; upper lip not enlarged and does not overhang lower one. Profile in nasal region bulges slightly.

Dewlap absent. Preorbital glands large. Hoof glands in the form of saccate folds on extremities, tarsal glands large, and metatarsal glands absent.

Color of summer coat an intense brown, becoming lighter in winter, even pure white in some forms. Legs not lighter in color than trunk. Color field on rear of thigh ("speculum") absent or small. Above the neck hair elongated and forms a mane. Color of juveniles uniformly dark (without light-colored spots). Female slightly smaller than male with somewhat smaller and less complex antlers. Teats four.

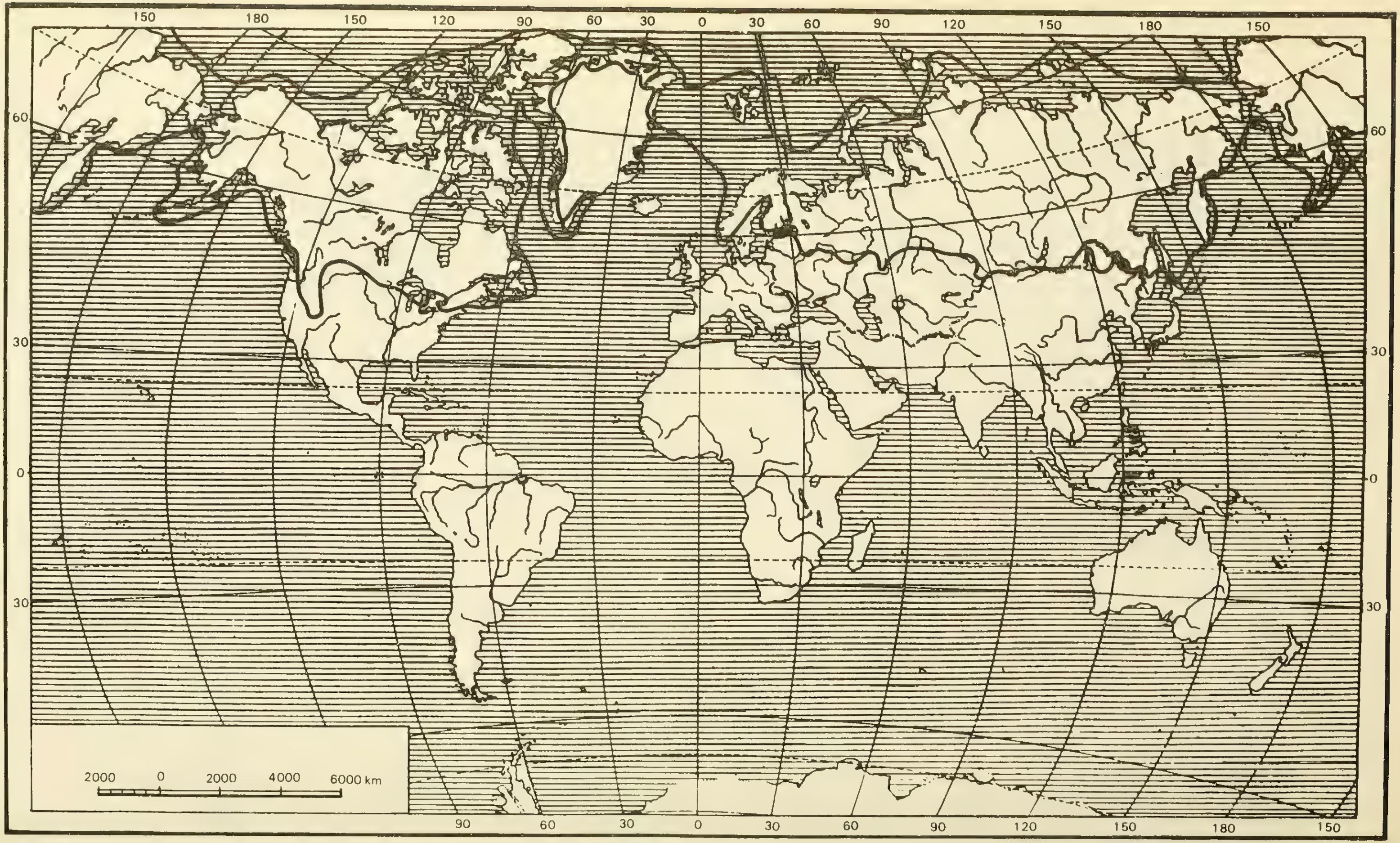
Reindeer live in the Arctic, partly in montane areas, tundra, and forests of the taiga type.

The range of the genus is associated with the tundra and taiga zone and can be divided into two parts—American and Eurasian. In North America the range (reconstructed) covers the northern half of the continent south to Newfoundland, Lake Superior (about 45° N lat.), Lake Winnipeg (around 50° N lat.), and the Rocky Mountains.

In Europe the range (reconstructed) in the historic past covered the Scandinavian Peninsula and proceeded south to the line running from the Gulf of Finland to the Moscow district and to the Sura and the southern extremity of the Urals. In the Trans-Ural and Western Siberia the southern boundary of the range runs along the southern edge of the taiga (roughly along 55 to 56° N lat.), covers the Altai, Sayan and Tuva mountains (including Tannu-Ola), Hobsogol region of Mongolia (around 50 to 51° N lat.), Trans-Baikal (apart from the steppe and forest-steppe regions), and northern taiga parts of northeastern China, and then through the northern half of the Ussuri territory to the Tatar Strait at 47 to 48° N lat. Reindeer occur throughout all of Sakhalin. In the north the range of the genus includes Spitsbergen, Novaya Zemlya, Franz Josef Land, Severnaya Zemlya, Lyakhovskiy, and the New Siberian Islands.

On the whole the range of the genus forms a typical circumpolar distribution in the northern hemisphere. It is significant, however, that it is associated with both high arctic, tundra, and taiga zones, i.e., represented a combination of circumarctic and circumboreal ranges. At present the above reconstructed range has changed considerably at some places (North America and Europe). The changes are particularly significant in the southern boundary, which has greatly shifted northward (see description of the range of *R. tarandus*).

The genus *Rangifer* occupies an extremely isolated position in the subfamily. It exhibits no distinct close affinities with any other genera of the subfamily although some characteristics (for example,


150
180
150
120
90
60
30
0
30
60
90
120
150
180
150
60
30
0
30
2000
0
2000
4000
6000 km

301

Fig. 96. Reconstructed range of reindeer genus *Rangifer* H. Smith and geographic range (reconstructed) of reindeer species, *Rangifer tarandus* L. (scale in km). V.G. Heptner.

structure of the vomer) do bring it close to some species of deer of northern and southern America. On this basis it is sometimes placed in the same subfamily (Neocervinae; Carette, 1922) as the American genera *Mazama, Pudu, Blastoceros,* and *Odocoileus,* and isolated from *Alces* and *Capreolus.* It has also been included under the Cervinae. Some older researchers suggested isolating *Rangifer* in a special subfamily, while some contemporary taxonomists have placed it as a special tribe within the Odocoileinae. All these classifications are less natural than the traditional one, recently confirmed by paleontological data (Simpson, 1945). Hence the traditional taxonomic placement of genus *Rangifer* is honored here.

In origin, importance, and typical expression of all characteristics, the genus *Rangifer* is the youngest of all genera of Odocoileinae or even Cervidae. It evidently evolved early in the Pleistocene in the southern and temperate parts of North America, from whence fossil forms associating it with other Odocoileinae are known (*Morenelaphus; Rangifer fricki*—Mexico). The genus acquired its present status in the mid-Pleistocene and later its members scattered 302 extensively throughout northern Asia, Europe, and North America, acquiring a circumarctic and circumboreal range. In view of the climatic peculiarities of the Glacial period, the range of the genus changed markedly, notably advancing far south. The occurrence of *Rangifer* with humans (sketches, sculptures, etc.) is known throughout central and western Europe, including England, Ireland, France, northern Spain, the Ukraine, and Crimea. All finds are of the present-day species.

A very large number of species have been described in the genus. Even in the 1920's as many as 13 species (!) of reindeer were reported by some authors for North America alone (Anthony, 1928); others even now acknowledge 4 (Miller and Kellog, 1955) or at least 2 (the tundra *R. arcticus* and woodland caribou *R. caribou*). For the Old World some authors in the last decade have recognized 5, 3, or 2 species. But in reality only one species exists—*R. tarandus*—which represents 5% of the species of the subfamily.

Rangifer are important table and game animals caught for their meat and hide. Some peoples in northern North America still depend on them for survival.

Rangifer are found in both wild and domesticated states.

In the Soviet Union only one form of reindeer is found—*Rangifer tarandus* Linnaeus, 1758—representing 0.3% of species of Russian fauna.

In the Soviet Union *Rangifer* inhabit high Arctic regions and tundra, taiga (mostly marshy), and highland (mountain tundra belt) zones of Siberia and Far East mountain ranges.

These animals represent table animals in the Soviet Union, which at places enjoy, or have enjoyed, great importance for the local people (western Siberia tundra). In parts of their range reindeer hunting is banned. They are raised as domesticated animals in large numbers, mostly in the tundra zone (extremely low level of domestication). (V.H.)

REINDEER[288]

7. ***Rangifer tarandus*** **Linnaeus, 1758**

1758. *Cervus tarandus.* Linnaeus. *Syst. Naturae,* 10th ed., vol. 1, p. 67. Mountains of Swedish Lapland.[289]

1784. *Cervus sibiricus.* Schreber. *Säugethiere,* pl. 248, C. The name has no nomenclatural significance (used in a descriptive sense and not as a binomial name).

1788. *Cervus tarandus, a rangifer.* Gmelin. *Syst. Nat.,* 13th ed., vol. 1, p. 177.

1822. *Cervus guettardi.* Desmarest. *Mammalogie,* vol. 2, p. 447.

1827. *Tarandus lapponum.* Billberg. *Syn. Faunae Scand.,* vol. 1, p. 22. Renaming of *C. tarandus* Linn.

1828. *Cervus tarandus schottingi.* Sternberg. *Isis,* p. 482.

1842. *Tarandus borealis.* Rüppel. *Mus. Senkenberg,* vol. 3, p. 183.
303 Substitute for *R. tarandus* Linn.

1852. *Tarandus furcifer.* Baird. *Rep. Comm. Patents,* vol. 7, *Agric.,* p. 109. Substitute for *R. tarandus.*

---

[288] [Literally, northern deer]; this is a bookish name. The popular name at places also inhabited by elk, maral, or izubr is simply "deer". At places where reindeer husbandry has developed they are usually recognized as domesticated and wild animals. Among reindeer farmers (Saams [northern peoples of Kola Peninsula], Nenetz, and Komi), many names are used for the different sexes and age groups of domesticated reindeer. Many have come into the Russian language with some modification. Some (not all) are used for wild reindeer. Thus, the male is called a bull, "khor," "poroz," or "irvas"; the female is generally "vazhenka", or from the age of one year and three months to two years and three months—"vondelka". Calves in first coat (up to August) are called "pyzhik," in August and September "neblyui," yearlings "lonchak," and so on. There are also several hunting terms based on the relation of the animal to the herd: "reut," "lonely irvas," "fugitive," and others (Semenov-Tyan-Shanskii, 1948). Different terms are used at different places. Thus, in Taimyr the male is called a "poroz," in Lapland "irvas," and so on.

[289] During the time of Linnaeus the Swedish state included Sweden, Norway, and Finland. This reference applies essentially to the northern part of the Scandinavian Peninsula.

1866. (*Rangifer arcticus*) var. *sibiricus*. Murray. *Geogr. Distr. Mammals*, p. 153. Siberia, east of the Lena.[290]

1898. *Rangifer tarandus typicus*. Lydekker. *Deer of All Lands*, p. 38.

1902. *Rangifer tarandus* var. *cylindricornis*. Camerano. *Mem. R. Acad., Torino*, vol. 51, p. 167. Renaming of *R. tarandus*.

1903. *Rangifer tarandus pearsoni*. Lydekker. *Proc. Zool. Soc. Lond.*, 1902, vol. 2, p. 361. Novaya Zemlya.

1909. *Rangifer tarandus fennicus*. Lönnberg. *Arkiv f. Zöol.*, vol. 6, no. 4, p. 10. Torne in Finnish Lapland.

1912. *Rangifer phylarchus*. Hollister. *Smiths. Misc. Coll.*, vol. 56, no. 35, p. 6. Southeastern Kamchatka.

1915. *Tarandus rangifer lenensis*. Millais. *Big Game of Asia and North America* (*The Gun at Home and Abroad*), vol. 4, p. 219. Lena delta (wild reindeer).

1915. *Tarandus rangifer chukchensis*. Millais, Op. cit., p. 220. Lena delta (domesticated reindeer).

1915. *Tarandus rangifer yakutskensis*. Millais Op. cit., p. 222, Yakutia (domesticated reindeer).

1915. *Rangifer tarandus buskensis*. Millais. Op. cit., p. 222. "Bask mountains near Semipalatinsk," thought to be the Altai (see note on p. 323).

1931. *Rangifer articus asiaticus* Jacobi. *Zool. Anz.*, vol. 96 (Ergänzungsband), p. 85. Substitute for *sibiricus* Murray as [Jacobi] 304 presumed it preoccupied by *sibiricus* Schreber. Kolyma (type a domesticated animal).

1932. *Rangifer angustirostris*. Flerov. *Trudy Soveta po Izucheniyu Proizvodit. Sil., Seriya Yakutskaya*, no. 4, p. 8. Barguzinsk range, balds between the Bol'shoi Chevyrkui and Bol'shaya Bannaya Rivers.

1933. *Rangifer tarandus valentinae*. Flerov. *Journ. Mamm.*, vol. 14, p. 336. Upper course of the Chulyshman River, southeastern Altai.[291]

1933. *Rangifer tarandus setoni*. Flerov. *Journ. Mamm.*, vol. 14, p. 337. Sakhalin.

1936. *Rangifer tarandus silvicola*. Hilzheimer. *Zeitschr. f. Säugetierk*, vol. 2, p. 155. Olonets province.

1936. *Rangifer tarandus transuralensis*. Hilzheimer. *Zeitschr. f. Säugetierk*, vol. 2, p. 155. Konda River, western Siberia. (V.H.)

---

[290] Flerov (1952) designates Berezov in western Siberia as the type locality.

[291] Not "northeastern Altai" as stated by the author.

Diagnosis

Genus *Rangifer* contains only one species.

Description

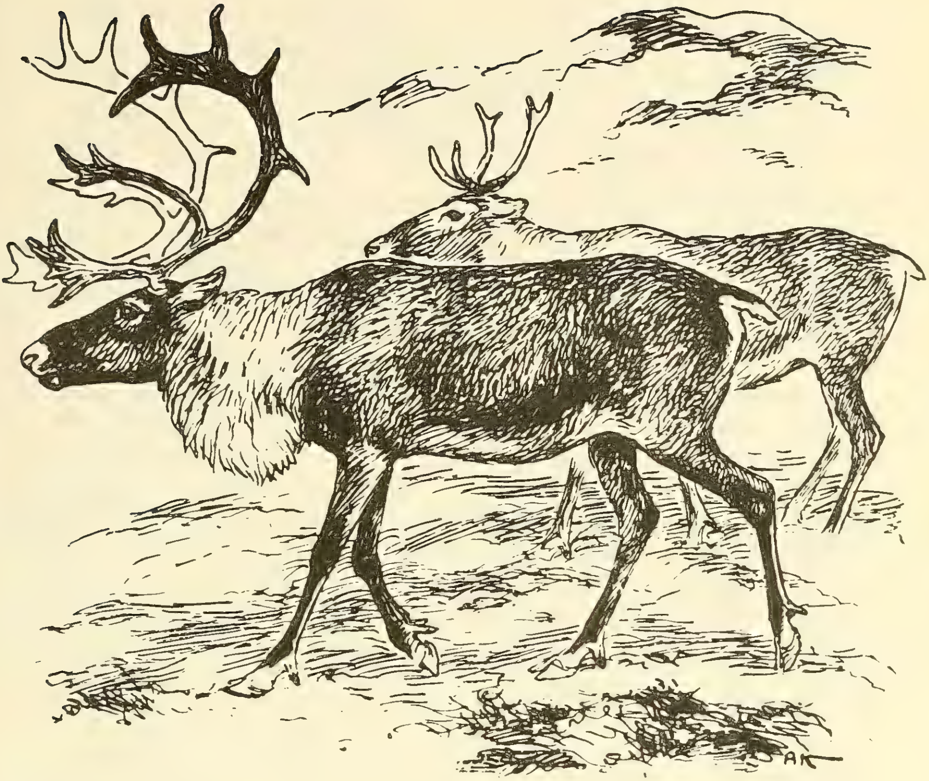
Size moderate. Build quite slender but differs characteristically and greatly from that of red deer (genus *Cervus*). Trunk elongated, neck fairly long and, because of intense hair growth, appears thick and massive, and legs relatively short. Head proportionate. Head and neck usually set low as though stooping. On the whole reindeer appear stocky and shortlegged and far less slender and beautiful than other deer. They lack grace of movement. If the general appearance of red deer (genus *Cervus*) is taken as typical of deer, then elk with their long legs and short trunk would represent an extreme deviation on one side and reindeer on the other; then it is the antipode of the elk.

Withers slightly raised but devoid of hump and not higher, or only slightly higher than croup, and back straight. Posterior part straight or slopes gently. Tail short but slightly longer than ears and visible in an active animal. Females somewhat smaller and weaker than males and have a less massive trunk. Head of reindeer, although proportionate, slightly stretched. Head relatively low in cerebral region and only slightly constricted toward tip, while muzzle appears somewhat enlarged but not to the extent as in elk; upper lip not enlarged and does not overhang lower one. Profile of nasal region bulges slightly. Ears relatively small and blunt at tips. Eyes small.

All of metapodial region of limbs relatively large and massive. Hooves of middle digits large, broad, flat, and highly curved (bracket-shaped, nearly semicrescent from below). External outlines of both hooves together form an almost true circle. Hooves of lateral digits large, set low, and touch the ground while walking. Lateral digits functional, particularly on soft ground (snow and marshy soil), providing a significant additional support and carrying a large load. Corresponding bones, especially first phalanx, quite massive. Contact surface of feet in reindeer in absolute terms, and especially in relative terms, far greater than in other deer—four times more than even in elk (load per cm^2 in elk around 560 g and in reindeer around 140 g; Semenov-Tyan-Shanskii, 1948). All digits mobile and with wide movement, which further enhances contact area.[292]

---

[292] A dry clicking sound is heard during the movement of adult reindeer. The source of this sound is not really known but it does not arise from the clicking of the



303 Fig. 97. Reindeer, *Rangifer tarandus* L. Sketch by A.N. Komarov.

305 Newborns and juveniles in the first few months stand somewhat higher on their legs than adults, but are not as tall as red deer or elk.

Reindeer antlers[293] grow to very large proportions and are relatively larger than those of other Russian deer. However, the beam and tines are thin and antler weight does not exceed 11 to 12 kg. Very often they are small and weak and devoid of the characteristic backward and forward bends; usually in the form of an almost straight or slightly bent beam with a small number of tines set upward and backward. Among domesticated reindeer antlers often reach unusually large dimensions, far larger than those in most specimens of a wild

---

hooves against each other. Among other deer this phenomenon occurs only in *Elaphurus davidianus* (Pere David deer), in which the contact surface is also relatively greater; this species inhabited marshy localities in China.

[293] For a description of skull and antlers, see characteristics of the genus.

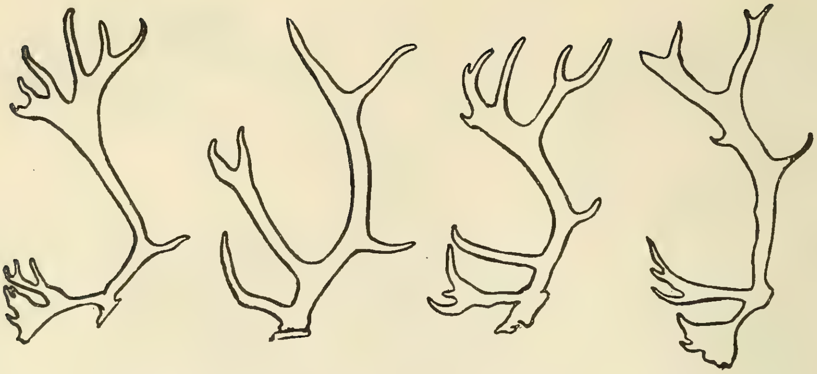


Fig. 98. Some types of reindeer (*R. t. tarandus*) antlers from the European part of the USSR (Arkhangel'sk and Vologda districts) (from Jacobi, 1931, with some modifications).

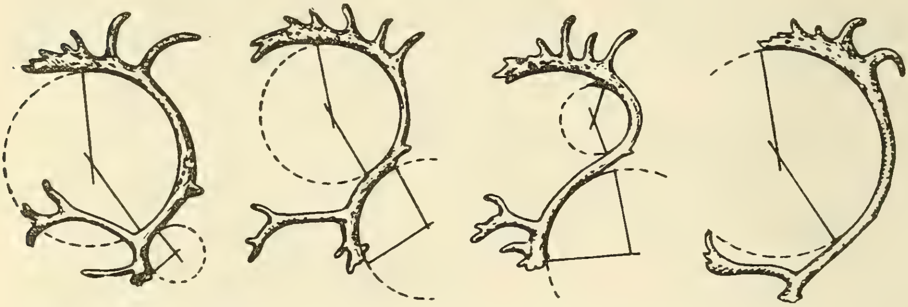


Fig. 99. Scheme of structure of reindeer antlers (from Herre, 1956).

population, sometimes creating an exaggerated impression of their size in the species.

In general, however, even if antlers are well developed and large, they are extremely diverse in length of beam, its flexure, number and size of tines, degree and number of palmate enlargements, structure of palmate portions of the first and second tines, spread, and so on. The diversity of reindeer antlers is more than that of other Russian deer and even greater than that of elk. Sometimes a distinction is made between antlers of the "forest" type with a relatively small beam and a large number of tines set throughout the antler length or on much of it, and antlers of the "tundra" type. In the latter the beam is very long and thin, carries a large brow and bez tines with palmate portions, and is nearly devoid of tines almost throughout its length, exhibiting them only in the terminal portion. The form of the beam as well as the direction of its bend are extremely variable
306 (Figs. 98 and 99). In addition to significant individual variability,

antlers exhibit some geographic variability.[294]

Antlers of females are similar to those of males but smaller and lighter. Almost throughout the range, but as rare exceptions, solitary hornless female "vazhenka" are encountered. In the Altai and Sayans the percentage of hornless females is higher, reaching 25 to 33 (see below).

The hair coat is typical of deer but all its characteristic features more distinctly manifested than in other Russian species, including even elk. This is true primarily of the winter coat and is associated with habitation in high latitudes. Winter hair is extremely long, and guard hairs reach a length of about 50 mm on the sides, 90 mm on the back, and 100 mm on the sacrum. Hair on the neck is even longer, about 300 mm, and forms a dense long mane, imparting to the neck such thickness and bulk that it appears almost as thick as the trunk. Almost 90% of the hair thickness is accounted for by a highly vacuolate core with air-filled cavities. Therefore the hair is extremely brittle. Hair on the legs is short, highly resilient and strong, and capable of withstanding wear during movement in snow. Long, dense, but strong hair around the hoof enlarge the area of contact of the hoof. The "brush" of long and very strong hair between the hooves also serves the same purpose. It also prevents slippage. Hair on the head is relatively short. It completely covers the nasal portion, leaving not even a minute area bare. Under the dense cover of coarse hair lies a dense, soft, crinkly fur which is not visible outwardly. All these together make a warm, strong, air-filled (within and between the hair) hair cover, impermeable to air.[295] This structural feature imparts to the animal a special buoyancy and thus reindeer are the best swimmers among all Russian deer.

The summer hair is considerably shorter and softer with weakly developed air cavities. The mane is not so long and hair around the hooves is absent. In newborn and one-month-old animals the fur is very soft and tender and air cavities absent or very poorly developed.

The summer coat is uniform in color[296] almost throughout the body and coffee-brown, grayish-brown or ash-brown. The lower surface of the tail and the inner surface of the thigh around the tail and slightly below it are white and form a small speculum. The hair surrounding the hoof is white. The sides of the neck are light, brownish-white, dirty white, or even white, and the hair on the lower side of the neck (mane) white. Sometimes (Altai) a light-colored, even white, patch occurs on the sides. The summer coat apparently is fairly uniform in color throughout the range and shows relatively insignificant individual variability.

---

[294] This phenomenon has not been studied for Russian deer and Soviet researchers have deliberately ignored the structural characteristics of antlers. This is as illogical as exaggerating the importance of antler structure in taxonomic classifications, as done by some foreign zoologists. Antlers of domestic reindeer, which have not been subjected to selection, are more diverse and larger than those of wild reindeer.

[295] Reindeer fur used in apparel (parka, mittens, etc.) and in mattresses is very warm and wind proof, and not at all durable; it usually lasts for no more than one season.

[296] Good descriptions of the color of reindeer, including their individual, sex-related and geographic changes are not available in literature. Even data on wild reindeer available in museums is extremely scanty. Hence information on color is perforce brief and schematic.

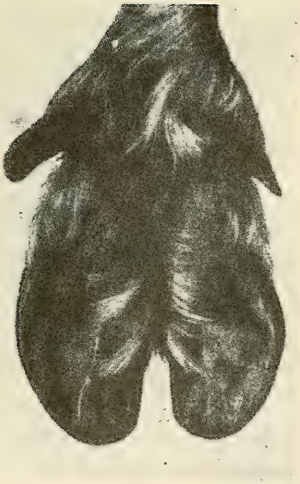
The winter coat is fairly variegated, with light- and dark-colored areas (more variegated than in other Russian deer) and, unlike the summer coat, exhibits extreme individual variability. Evidently geographic variability is also considerable. In some places coloration is quite dark, but almost white or even totally white in others. In typical reindeer, dark, brownish-gray hair is found in the upper
307 parts of the head, back, legs, and croup in winter. The lower half of the head is light-colored, the neck and mane white, sometimes with a brownish tinge, hair on the hooves white, a large light-colored, sometimes white, spot occurs on the side, and a broad dark band corresponding in color to that of the back runs down the lateral side from the region of the elbow to the knee. The lower surface of the tail and the inner parts of the thigh around the tail and below are white and form a small speculum. This color scheme varies highly in intensity of the dark shades and purity and vividness of white coloration, as well as relative areas occupied by dark and white patches. This is relevant not only with regard to individuals but also to geographic variability.

Sex-related color differences are evidently absent or insignificant, but are possibly manifested distinctly in some areas.[297]

Molt occurs only once a year, commencing at the end of winter (March) and continuing almost throughout summer, being most intense in June and July. In July–August a short and dark coat of summer hair characterized by a dense growth of fur and short guard hair is fully evident. The winter coat mainly consists of lengthening of the long guard hair, which fully conceals the underfur. The long guard hair with its highly vacuolate core is of a lighter color, and thus the color of the animal itself becomes significantly lighter than in summer. The color may vary considerably in the course of winter. As a result of fading (especially at the end of winter) in the sun and wear and tear, the tips of the coarse hair, usually very dark, lighten

---

[297] Among males of Altai reindeer, compared to females, the white neck and sides stand out more prominently in the summer coat (F.D. Shaposhnikov, 1955).



307 Fig. 100. Hoof of foreleg of reindeer. Photograph by O.I. Semenov-Tyan-Shanskii.

and the overall coat coloration bleaches and may turn almost white even in relatively dark forms.[298]

The overall coloration of newborns and calves in their first few months (until the commencement of molt and the first winter coat) is a uniform brown or brownish-gray, being slightly lighter in the lower body surface; lower parts of the tail, throat, and inguinal region are light-colored. The ears are brown outside and whitish inside, and the anterior surface of the legs darker than the rear. A dark-colored band occurs along the back. As an exception (more often in southern Siberia), fairly large, light-colored patches may develop, which are neither distinct nor prominent.[299]

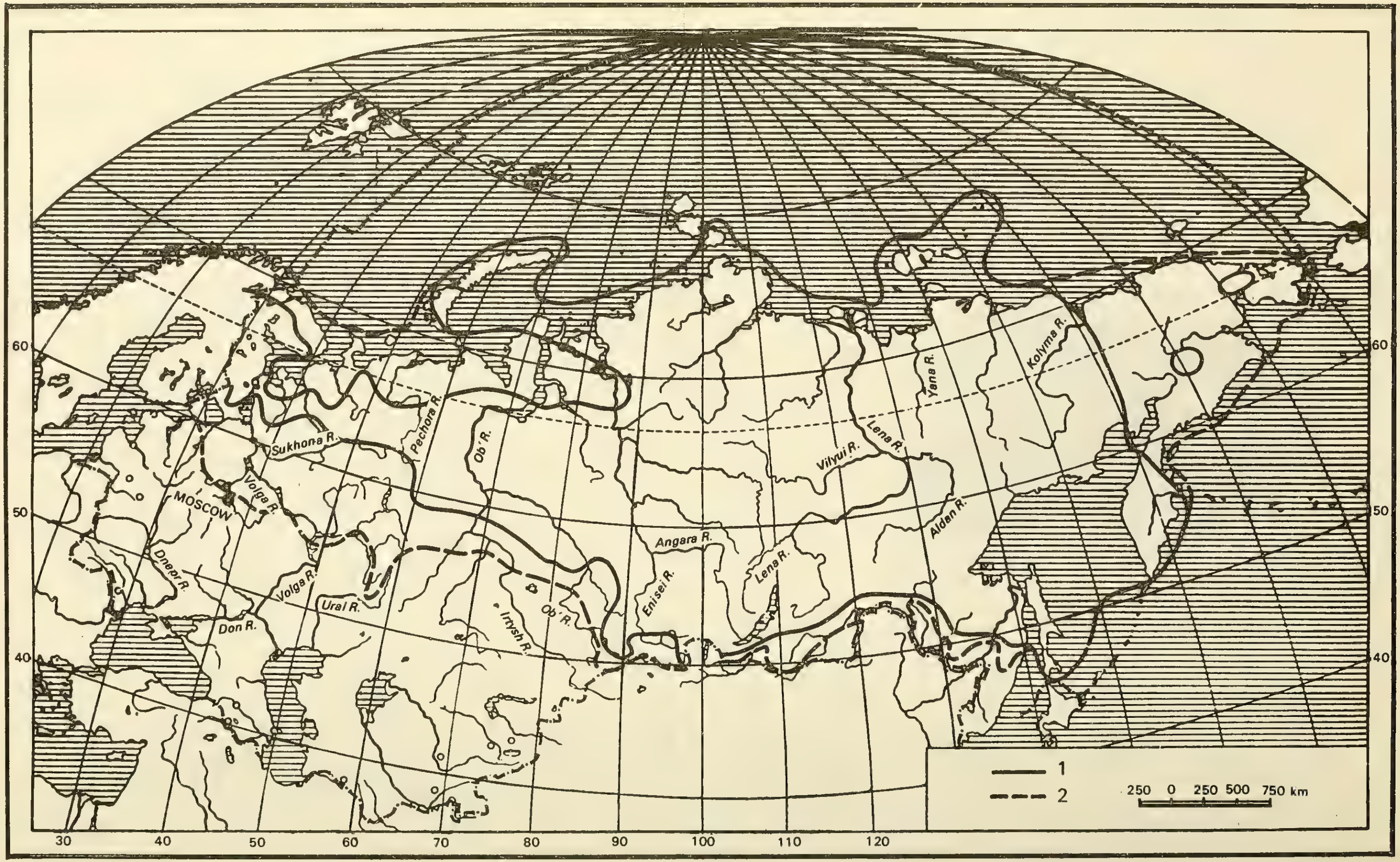
The dimensions[300] of adult males are as follows: body length 200 to 220 cm, height at withers 110 to 140 cm, tail length up to 20 cm, and length of ears about 13 cm. Weight in autumn 100 to 220 kg. Maximum skull length 335 to 438 mm. Females are somewhat smaller and much lighter than males. Their dimensions and weight

---

[298] It has been noted that reindeer pasturing in Lapland forests become less light in color by spring than those wintering in open mountain tundras (Semenov-Tyan-Shanskii, 1948). No doubt the sun exerts a greater effect in the open high-altitude Siberian mountain ranges. It is possible that some of the differences noticed between taiga reindeer and reindeer in some Siberian montane tundra are due to color fading.

[299] For skull characteristics see description of the genus.

[300] From the morphometric point of view wild reindeer are one of the least studied Russian ungulates and information available in literature about their body dimensions and weight is extremely scanty.


60
50
40
60
50
40
Sukhona R.
Pechora R.
Ob' R.
MOSCOW
Volga R.
Dnepr R.
Volga R.
Ural R.
Don R.
Irtysh R.
Ob' R.
Enisei R.
Angara R.
Lena R.
Vilyui R.
Lena R.
Yana R.
Aldan R.
Kolyma R.
1
2
250 0 250 500 750 km
30
40
50
60
70
80
90
100
110
120

reveal geographic variability. Newborns weigh 6 to 7 kg.[301] (V.H.)

309
Taxonomy

Rangifer tarandus is the only species of the genus.

Geographic Distribution

Reindeer are distributed in the arctic and taiga zones of the Old and New Worlds.

Geographic Range in the Soviet Union

The range in the Soviet Union probably represents about two-thirds of the range of the species and covers much of the territory of the USSR.

The boundaries of the reindeer range have undergone intense changes over the historic period. This is particularly true of the southern boundary. On the whole the range has steadily shrunk and its southern boundary withdrawn northward. This process was initially drastic and rapid and is still continuing in western Europe and the European part of the USSR.[302]

Material for deciphering range changes over the historic period up to the present is scarce indeed. Some scattered information is available for the European part of the USSR for the eighteenth, nineteenth, and partly twentieth centuries. This makes it possible to reconstruct the southern boundary of the range only for the recent period. In the distant past the range extended south in the European

---

[301] The weight of newborn fawns represents about 9% of the mother's weight, while that of elk fawns roughly constitutes 3.0 to 4.5% of the mother's weight (Semenov-Tyan-Shanskii, 1948).

[302] It has sometimes been assumed (Pidoplichko, 1951) that reindeer inhabited Central Europe at the beginning of our era. This is quite possible but Caesar's text (description of Hercynian forests), on which this assumption is primarily based, cannot be taken as conclusive. Roughly around that period reindeer did live in the Kiev district (Pidoplichko, 1951). Reindeer fossils are known in the western half of Europe as far as the Mediterranean Sea.

---

308 Fig. 101. Boundaries of distribution of reindeer, *Rangifer tarandus* L., in the Soviet Union (scale in km).

1—Recent (mid-1950's) boundaries of range (approximate and highly schematic at places); 2—reconstructed boundary at places where it does not coincide with recent. V.G. Heptner.

part of the USSR, farther than in the nineteenth century. Judging from the topographic features and biological characteristics of the animal, the boundary as a whole did not, however, advance particularly far south (see below).

It is also difficult to establish range boundaries precisely because the reindeer range has evidently undergone natural fluctuations over quite a prolonged period, extending over a few decades, as has been noted in the case of elk. Finally, as in the case of several large animals, the true boundary often cannot be established precisely because remains have been found beyond the supposed boundary, especially in the period of range enlargement. At the time of boundary recession some "islands" of habitation made up of small groups of animals could have been left behind.

European part of the USSR and Ural. The southern reconstructed boundary of the range given below pertains to the latter half of the nineteenth century right up to the end of the 1890's, often to the earlier decades of the present century. It could roughly be designed as the boundary around 1900. It reveals some southward thrust of the boundary, prevailing in the latter half of the century (see below). The peripheral points often depict sites not only of permanent habitation but also visitations.

At that time the southern range boundary in the European part of the USSR commenced on the southwestern shore of Lake Ladoga. Evidently, reindeer were absent in the Karelian Isthmus; they could have penetrated only into the northern part of the isthmus along the northwestern shore of the lake. From Lake Ladoga the boundary ran toward Lake Ilmen' (northern shore) and from there to Lake Seliger toward Ostashkov. Later it turned even more southeast, encompassing the region of Staritsa (around 56°30′; former Staritsa district) and the Kalinin region. From there the line proceeded south of Uglich (57°) and through the northeastern part of Moscow district (evidently forests north of Zagorsk)[303] ran toward Aleksandrov (known to occur also at Pleshcheev, or Pereslav, lake).

Farther away in the east the range boundary ran, in a manner not
311 completely understood, through the Vladimir Forest on the Lukh River (evidently its lower course, Trans-Klyazma Bor [pine grove]), reaching the Klyazma slightly below Vyazniki. In the stretch from Staritsa the boundary thus proceeded generally between 56° and 57°, but more closely to 56°. It is highly probable that at some places it

---

[303] ". . . the hide of a male reindeer, killed on February 18, [1881; V.H.] was found at the border of Moscow, Tversk, and Vladimir province in Aleksandrov district, near the village of Nupal'sk . . . In all, there were only five hides." (Lorents, 1881).

proceeded along 56° and ran even beyond it (Murom Forest), but there is no direct evidence for this; nevertheless some zoologists mark the boundary even more east [? south] of 56°.

East of the mouth of the Oka the boundary ran for some distance along the left bank of the Volga and later, short of reaching the mouth of the Kerzhents or somewhere around Kerzhents, crossed to the right bank and descending southeast (or southward) encompassed the Knyaginin region (about 50 km. due south of Kerzhents mouth), and later the forests in the Kurmysh region on the Sura (former Kurmysh district) lying east of Buinsk district on the Sviyaga (former Buinsk district). The boundary descended there down to 55° N lat. or even more south. This is the southernmost point of habitation of the species in the European part of the USSR (excluding the Urals).

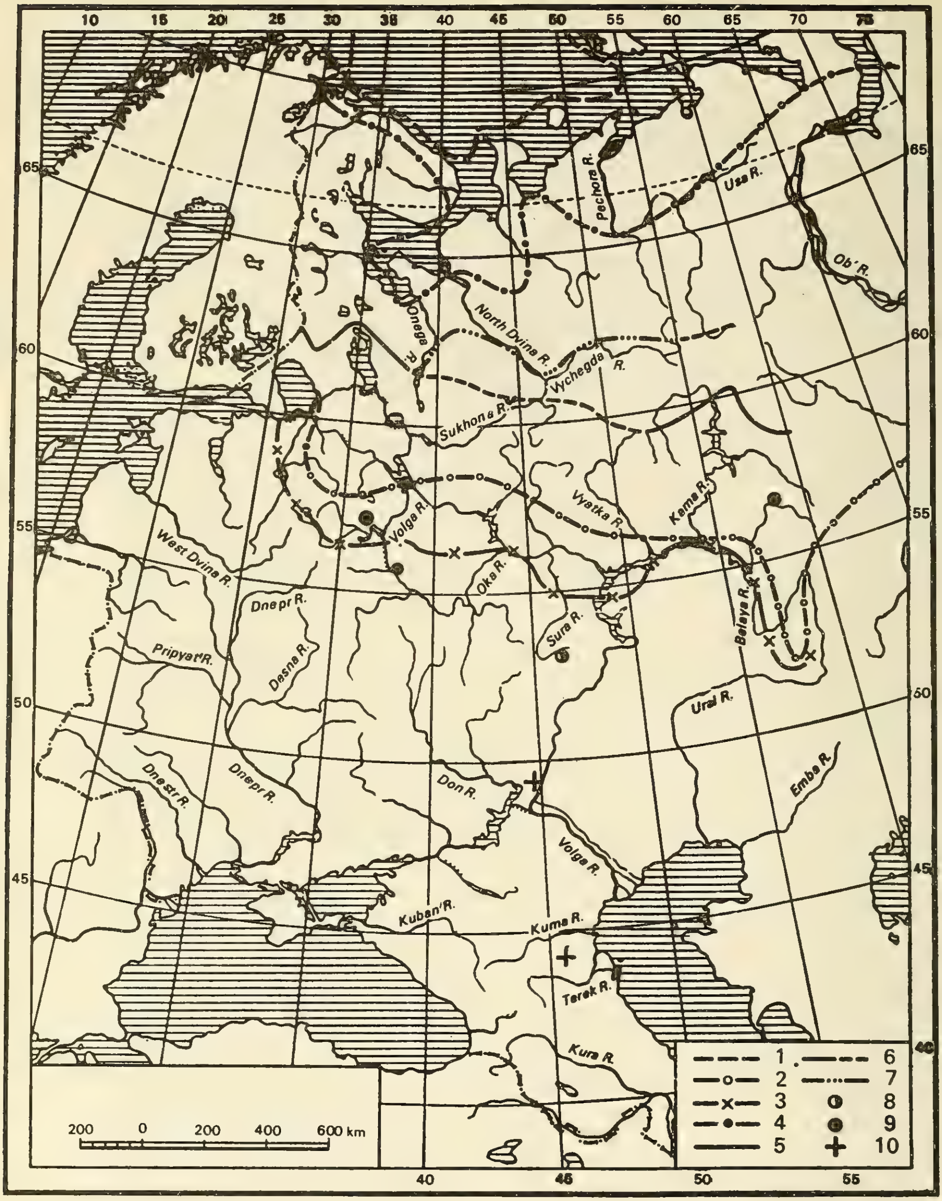
From Buinsk the boundary again crossed to the left bank of the Volga somewhere south of the Kama mouth and encompassed the Cheremshan district (Cheremshan Forest in the former Spassk canton). Later, it evidently shifted slightly northeast and, covering the Mamadysh and Elabuga regions, ran along the Kama to the mouth of the Beloe. From there the boundary line proceeded south along Ural foothills, not crossing to the west of the Beloe but almost reaching Ufa or running very close to it (55°). In the south along the Urals the range extended as far as 51°45′ and approached close to Orenburg.[304]

It is possible that in some centuries of the distant historic past the range at places, for example west of the forest zone, extended farther south than described above, but there are no reliable data to support this probability. Moreover, the topographic features of the south and the ecological properties of the species are such that its habitation more southward appears unlikely. In any case it was absent in the forest-steppe zone or encountered only in some limited northern sections such as the places mentioned above in the region adjoining the lower course of the Sura and in the southern Urals.

Mention is often made in literature about the former occurrence of reindeer in the former Sengilei district at 54° N lat., in the region of the source of the Sura at 53°, at Dubovka on the Volga (slightly above Volgograd at 49°03′), and even on the Kuma at 46°. These data unfortunately have been cited by one author from another without either checking the primary sources (Bogdanov, 1871—Sengilei

---

[304] The range boundary given is based mainly on data from Köppen, 1883; partly Turkin and Satunin, 1900; Eversmann, 1850; Bogdanov, 1871; Zhitkov, 1898; Satunin, 1895; Sabaneev, 1868; Bashkirov and Grigor'ev, 1931; and several other sources.


10
15
20
25
30
35
40
45
50
55
60
65
70
75
65
60
55
50
45
40
Pechora R.
Usa R.
Ob' R.
Onega R.
North Dvina R.
Vychegda R.
Sukhona R.
Volga R.
Vyatka R.
Kama R.
West Dvina R.
Dnepr R.
Oka R.
Sura R.
Belaya R.
Pripyat' R.
Desna R.
Ural R.
Dnestr R.
Dnepr R.
Don R.
Emba R.
Volga R.
Kuban' R.
Kuma R.
Terek R.
Kura R.
1
2
3
4
5
6
7
8
9
10
200
0
200
400
600 km
40
45
50
55

310 Fig. 102. Some changes in the range of reindeer, *Rangifer tarandus* L., in the European part of the USSR.

1—northern restored boundary; 2—southern boundary of area of regular habitation circa 1850 (Köppen, 1883); 3—southern boundary of distribution in second half of nineteenth century (some data for first half of century) and toward 1900; 4—northern boundary of distribution in the 1940's and 1950's; 5—established, and; 6—inferred southern boundary of distribution in the 1930's and 1940's to 1950; 7—southern boundary of distribution in the winter of 1955 to 1956; 8—southernmost point of occurrence of reindeer at the source of the Sura [River] in the seventeenth and beginning of the eighteenth century; 9—isolated areas near Krasnoufim, in the Mologa-Sheksnin interfluve (1925), and in Orshinsk Mokh (1938); 10—erroneous reports on the southern boundary of reindeer habitation in the past. V.G. Heptner.

district and Sura; Pallas, 1776—Dubovka and Kuma) and hence are highly distorted. All, with one obvious exception, should be discarded as proofs of reindeer distribution in the historic past. At Izmailovka in the Sengilei district reindeer antlers have been exposed after soil erosion together with rhinoceros bones and antlers of these "fossils" (Bogdanov, 1871). The past occurrence at Dubovka was only suggested by Pallas (1771). There is a creek there named "Olenii" [reindeer] from which reindeer antlers have been washed out. The region between the Volga and Don at these latitudes, even in the mid-1800's was solely a steppe region; forests occurred there, however, in the distant past in which reindeer might have lived. Along the Olenii creek itself forests survived even at the time of Pallas. Finally, Pallas found a favorable argument for the possible occurrence of reindeer at Dubovka in that, in his view, the animals during his time existed in the Caucasus and reached northward to the Kuma River.[305]

312 Information about the distribution of reindeer to 46° in the south is evidently based on data by Pallas about the Kuma, although he himself adduces no direct proof (furthermore, Kuma lay at 45°). Sometimes data for 46° are given without references to the region or are even ascribed to the Urals, which is not understandable at all since latitude 46° runs through the northern part of the Caspian Sea, Mangyshlak, and the Aral Sea.[306] Among the foregoing habitations the reference that deserves attention is the region of the Sura source at 53°. Evidently reindeer lived there in the seventeenth and probably even in the early eighteenth century (Bogdanov, 1871). The Sura basin even now is rich in forests, which were far more abundant in

---

[305] About the Caucasus, Pallas wrote (1776, p. 587) that "reindeer were present in the Caucasus mountains ("am Kaukasischen Gebürge") up to places along Kuma River ("bis um den Kuma-Fluss"), which the Kalmyks killed sometimes in winter at the edge of the steppe." Thus, Pallas has in view the distribution of reindeer from the Caucasus in the north up to Kuma and the southern parts of Kalmyk steppe (steppes on the right bank of Volga), and not in the south up to Kuma, as reported later by others based on his data. In his reports on the occurrence of reindeer in the Caucasus, Pallas, however, erred. There were no reindeer in the Caucasus. It is significant that in a much later report in *Zoographia* (1811) Pallas makes no mention at all about reindeer at Dubovka and in the Caucasus, which is quite far south in the European part of the USSR.

[306] According to Flerov (1935) ". . . in the Ural mountains it [reindeer, V.H.] formerly descended far south reaching to 52° N lat. and even to 46°." Strangely the basis of this thoughtless description was evidently provided by such a thorough investigator as Middendorff who stated (1867): "100 years ago reindeer reached there [Urals, V.H.] to 46° north" (Pallas, *Reise*, vol. 3, p. 597). Turkin and Satunin (1900) adduce from Middendorff the foregoing statement in quotation marks, supplementing it with data from Sabaneev for the Urals.

the past. These forests descend southward in a broad projection, even south of the Sura source, and directly join the northern Trans-Volga forests.

The above southern boundary line of the range of reindeer in the European part of the USSR indicates their maximum distribution in the south in the distant past. As stated above, this is the result of some enlargement of the range before the latter half of the nineteenth century. Around 1850 the boundary of permanent habitation of reindeer in the northwest commenced on the east shore of Lake Ladoga somewhere north of Olonets, crossed the Svir close to its mouth, and later turned south slightly east of Volkhov. Short of Lake Ilmen' it swerved southeast, intersected the Msta in its lower course and later in its upper course somewhere in the region of Vyshnii Volochek. From there, crossing the source of the Mologa and forming the southern boundary of the range, it turned roughly through the present Rybinsk reservoir in the east, crossing the Kostroma River slightly north of Buinsk, and later, slightly inclining southward, intersected the Vetluga roughly around 57°30′. From the Vetluga the boundary ran into the Vyatka, crossed it in the Malmyzh region, and ran to the Kama at 56°, slightly above the mouth of the Beloe. From there the boundary line turned to the Ufa River, intersected it roughly at latitude 55°30′, and went into the mountains. The range descended far south in a narrow band along the much higher interior sections of the mountains, reaching roughly 52° N lat. (Köppen, 1883).

Compared with this line, the boundary outlined above advanced southward to a distance of several tens to 100 or even 250 km (central Soviet territory). In all probability, however, actual advancement of the 1850 line of permanent habitation has most likely been minor. The reasons for range expansion are not clearly understood. Expansion (as in the case of elk at that time) occurred in spite of man's notably adverse influence.

The reconstructed northern boundary of the range reached everywhere up to the sea coast and the range covered islands falling in the European sector of the Arctic: Solovetskie, Kolguev, Vaigach, and the two islands of Novaya Zemlya. There were no reindeer on Franz Josef Land.

While prior to the nineteenth century, as stated before, there were considerable fluctuations in the southern boundary, the twentieth century was characterized by its very sharp and extremely rapid recession to the north, evidently exclusively as a result of the animal's destruction. Since the boundary fluctuated rapidly, even within a span of a few years, and information on the distribution of reindeer before the present century is very scanty, the contemporary boundary line, with the exception of a few places, can only be approximated. Precisely for the same reason the boundary cannot be shown for any given year. The discussion below, therefore, pertains to the 1930's–1940's and partly the 1920's.

In the west the southern boundary of the range commenced at the state boundary with Finland at the latitude of the northern extrem-
313 ity of Lake Onega. From there it descended sharply southeast, encompassing Suojarvi, and as sharply, forming an acute angle, rose northeast. It passed north of Lake Onega quite close to its shore. From there the line ran steeply southeast again, passing through Lake Vodl and extending toward the boundary of Karelia and the Arkhangel'sk district at 62°20′ or slightly more south. It thus encompassed the northeastern part of the Pudozh region (Stroganov, 1949; Marvin, 1950 and 1951). Slightly more east or southeast reindeer were known from the Kargopol region (V.Ya. Parovshchikov).

The boundary line farther east of the Dvina is not known. It evidently crossed the Dvina in the region of Velikii Ustyug.[307]

In the 1930's the southern boundary at the sources of the Vyatka and Kama passed through Kirs on the Vyatka roughly at 59° N lat., ran east across the Kama (Lobachev, 1930) and, in a manner not clearly understood, to the Urals, along which reindeer were distributed in the south up to 59° (Shvarts, Pavlinin and Danilov, 1951). Mentions of reindeer occurrence in the Urals at 56° (Druri, 1949; Flerov, 1952) thus do not correspond to the actual situation.

Some information is available about the occurrence of reindeer north of these places in the basins of the Vychegda, Pechora, and Kama—in the Storozhev, Ust'-Kulom, Ust'-Nema on the Vychegda, Ukhta, Ilych, and Pechora-Ilych preserve in the Pechora basin, and on the Vyshera, and at other places nearby (Lobachev, 1932; Teplov and Teplov, 1947; Druri, 1949).

Boundary recession was naturally uneven and generally represented a complex process so that withdrawal of the line can only be discussed in very general terms. Furthermore, the withdrawal of some, albeit small, groups of animals into particularly deserted or not easily accessible places could have preserved them even when the boundary stabilized to a fairly normal level and continuous habitation receded farther away. Evidently a small population of reindeer persisted in the east for some time in the Krasnoufim (Kuklin) region and in the west in the dense forests between the lowermost courses of the rivers Sheksna and Mologa at the site of the present Rybinsk reservoir. There the animals continued to exist at least up to 1925 (Shchegolev, 1925; cited from Kaletskaya, 1957). Other such relict pockets also existed. It is significant that even in 1938 small numbers were present at Orshinsk Mokh, an extensive marshy area northeast of the city of Kalinin (S.M. Uspenskii).

---

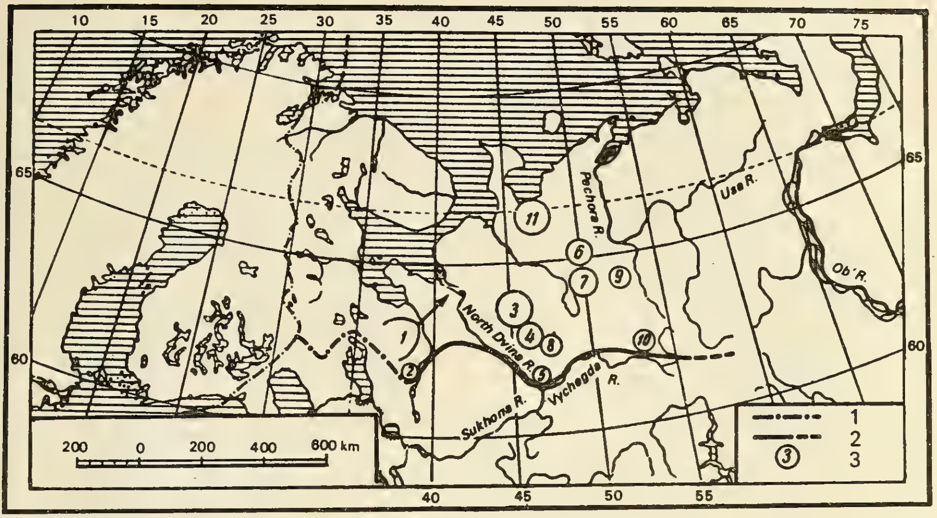
[307] Reindeer existed "in the forests of the Ustyug district in the region of the Lila and Chagodishcha Rivers" (Druri, 1949; information for 1925).

Later the southern boundary withdrew even more northward and in the winter of 1955 to 1956 passed through the Kargopol region and Lake Lacha, through the Uftyug River region, entering the Northern Dvina below Sol'vychegodsk, and the regions of Storozhev and Ust-Kulom on the Vychegda (V.Ya. Parovshchikov; see below). How it extended along the Urals is not known.

The northern boundary of the contemporary range in the European part of the USSR also varied intensely and receded far south. In the Kola Peninsula the range receded from the sea coast and the animals survived only in the interior parts of the peninsula. Later the boundary ran along the White Sea without including the Solovets Islands, then ran on to the mainland in the southern part of Onega Bay, probably somewhere at the 36th meridian. Moving away from the sea coast it ran east roughly along 64° N lat. and at the Dvina slightly south of Arkhangel'sk. Roughly at the same latitude it intersected the Pinega in the Karpogor region. From there it rose steeply northward, intersected the Mezen', encompassed the Om' and Snopa River basins, and ran along them toward the coast of Cheshskaya Bay. From this bay it took a sharp turn southeast into the region of the upper course of the Tsil'ma (Leshukon region) and into the Ukhtin region at the source of the Vym' roughly at 64° (according to data of V. Ya. Parovshchikov in the winter of 1955 to 1956; see below). Later the boundary line turned northeast into the region of the lower reaches and mouth of the Usa on the Pechora and from there south of the vicinity of Baydarats Bay (Druri, 1949). It is possi-
314 ble that the boundary nowadays runs differently in the section to the east of the Vym'. In any case the tundras of the European part of the USSR—the Kanin, Malozemel', and Bol'shezemel', apart from the tiny section at Cheshskaya Bay, were already devoid of wild reindeer.

A comparison of the present (mid-1950's) northern and southern boundaries of the range reveals that the latter now represents essentially a negligible residue of the former range of reindeer and extends in the European part of the USSR in the form of a narrow band along the northern parts of the forest (taiga) zone. This band is somewhat broader in the east and west (in Karelia).

In fact, however, reindeer distribution in this belt was not continuous. Only pockets, sometimes closely continuous, but often



314 Fig. 103. Some details of the distribution of reindeer, *Rangifer tarandus* L., in the northern sector of the European part of the USSR in the first half of the 1950's (scale in km).

1—southern boundary of the range of reindeer in Karelia in 1950; 2—southern boundary of reindeer distribution in Arkhangel'sk and partly in the Komi Autonomous Soviet Socialist Republic in the winter of 1955 to 1956; 3—individual pockets of reindeer occurrence in the winter of 1955 to 1956 in Arkhangel'sk district and partly in Komi Autonomous Soviet Socialist Republic (from V.Ya. Parovshchikov; explanations in text). Arrow points to direction of transgressions toward the lower course of the Northern Dvina. V.G. Heptner.

greatly separated from each other, existed. Moreover, the numbers of animals in these pockets varied greatly but were generally few. By and large only a small part of the range was actually colonized and the population of the species was very small. In some cases animals from pockets of fairly permanent habitation roamed quite far and were seen at places where they were ordinarily absent.

Thus, in the winter of 1950 to 1951 a small group from the southwest migrated into the region south of Arkhangel'sk (Tundra Station), evidently covering a distance of about 150 km (V.Ya. Parovshchikov).

The following places of reindeer occurrence in Arkhangel'sk district and partly in the region of the Komi Autonomous Soviet Socialist Republic are known for the winter of 1955 to 1956 (V.Ya. Parovshchikov).[308]

---

[308] Numbers correspond to those given on the map (Fig. 103). Figures in parentheses indicate roughly the number of animals in that place.

1) Southwestern part of the Onega region and territory of the Yangor government village in the Priozernyi region;

2) the Kargopol region (50);

3) Upper courses of Pim and Vashka Rivers (entering the Pinega on the left at the boundary with the eastern Toem' region) in Karpogor region (400) and the Zhert' and Seivas creeks (right tributaries of the Pinega) at the boundary of the eastern Toem' and Udor regions;

4) Gorkov and Vyisk government villages in eastern Toem' region (large numbers);

315 5) Along the Lakhoma tributaries—the Saimyi and Vaimug in the Krasnobor region (Beloslud, Berezonavolots, and eastern Uftinsk government village);

6) Northeastern corner of the Leshukon region;

7) Northeastern Udor region;

8) Southern part of the Udor region (upper course of the Vashka River);

9) Upper courses of the Vym', Kedva, Shomukova, and Toi-yu Rivers in Ukhtinsk region of Komi Autonomous Soviet Socialist Republic (rather small herds);

10) the Storozhev and Ust-Kuloma regions of the Komi Autonomous Socialist Republic;

11) Om' and Snopa River regions, from the shores of Cheshskaya Bay to the upper courses (herds of 5 to 10 to 100 to 200 animals).

The disposition of pockets of reindeer distribution described above reveals that the current European range of reindeer can be divided into essentially two parts—one east of the Northern Dvina and another west of [Lake] Onega. The latter occupies Karelia and extends into the Arkhangel'sk district only insignificantly. It is evident that the separation and isolation of Karelian and Pri-Ural regions is taking place and will proceed rapidly. The present-day state of the reindeer range positively indicates that in the European part of the USSR it is on the threshold of total and rapid disappearance. Only the immediate implementation of special measures can save it.

The reasons for this are more the innate ecology of reindeer and restriction [of their habitat] than direct extermination, although the latter also plays a very important role. Unlike elk, for which burned-out and felled forest sections, young plantations, etc. represent a very favorable environment, fires, fellings, and clearance of forests, and in general any disturbance to their normal state, is of mortal consequence to reindeer. This explains how a sharp population increase and range expansion of elk leads to an exactly opposite situation in the case of reindeer.

Asiatic part of the USSR. For want of adequate information it is even more difficult to establish the southern boundary of the reindeer range in Siberia and the Far East than in the European part of the USSR. This boundary can be plotted only roughly and its chronological correlation is possible to a very limited extent. The more accessible early zoological evidences mostly pertain to the end of the first half and middle of the nineteenth century.

There is every justification to assume that in western Siberia in the distant past reindeer probably occurred up to the southern boundary of the forests and the northern boundary of the forest-steppe. Thus the southern boundary of the range between the Urals and Tobol'sk ran along the latitude of Kurgan i.e., slightly south of, or along, 56°. However, at the end of the latter half of the last century reindeer did not descend south of the mouth of the Tavda (around 57°40′). At this same latitude they were confined along the left bank of the Tura. Along the right bank of the Tura they were even found in Pushkarev, south of Turinsk, roughly near 57°50′.[309]

Between Tobol'sk and the Irtysh the boundary evidently deflected slightly northward, passing probably along 57°. Beyond the Irtysh it continued into the Novosibirsk district and reached the Barabinsk steppe at 55° in the south, i.e., roughly Lake Chany.[310] From there the boundary crossed somewhere into the Novosibirsk district on the right bank of the Ob', turned steeply southeast, and later south in a manner not yet established. Encompassing the Salair ridge (reindeer were indicated as occurring particularly in the region of the town of Salair and on Salair ridge even in the 1870's; Finsh, 1879), it descended toward the Altai, running on the middle or lower
316 course of the Biya. Turning southwest from there it encompassed the Altai uplands, probably including the Katun' Belki [Alps], surrounded the Argut basin (southern tributary of the Katun') from the south and east, and ran toward the state frontier.[311]

---

[309] Based on data from Slovtsov (1892).

[310] In the middle of the last century reindeer were sighted at 55° in the Barabinsk steppe almost every year during their winter migrations (Middendorff, 1867). Data on the southern boundary of the range between the Urals and Ob' as given by Middendorff (1867, p. 959) are inconsistent and evidently erroneous, for example, the total absence of reindeer in the whole of the Irtysh basin and on the left bank of the Ob' below the Narym and south of 60°. Several authors have based their works on the data of Middendorff in the original form or as reported by others, which has led to further confusion.

[311] According to Middendorff (1867) and Gebler (1837). The former range in Altai has been studied very little. Gebler doubted the presence of reindeer in the Katun' Belki and assumed their existence along the tributaries of the Argut, i.e., Dzhasater and Alakha. He himself points out the abundance of reindeer east of the Chulysh-

The present-day southern boundary in western Siberia likewise can only be approximated. Commencing in the Urals at 59° (Shvartz, Pavlinin and Danilov, 1951), it continues into the lower course of the Kuma (right tributary of the middle course of the Konda) and crosses the Irtysh below Tobol'sk roughly around 59°. Inclining farther slightly southward, it encompasses from the south the whole of the Dem'yanka basin, runs to the sources of the Vasyugan and Parabeli, and encompasses almost the whole of Chai basin. At the sources of these rivers the boundary turns slightly northeast and crosses the Ob' below the mouth of the Tom', roughly midway to the mouth of the Chulym. Running further along the Chulym toward the mouth of the Kiya, it turns south, encompassing the Kuznetsk Alatau. Roughly around 54° it turns southwest, encompassing the southern parts of the Salair ridge in the basins of the Mras-Sa and Kondoma Rivers and along the upper course of the Tel'bes. From there it turns south into Pri-Telets (eastern) Altai.[312]

In Altai the range covers the basin of the right tributary of the Biya, i.e., the Lebed', in the north. The western boundary there comes very close to Biisk, especially near the mouth of the Lebed' at Turochak, but does not reach Biisk itself. Farther south reindeer are present in the mountains north of Lake Telets and in the mountain range standing over Lake Telets on the east and along the Chapchal (Shapshal'skii) range, extending southward along the right bank of the Chulyshman toward its source. There animals inhabit the region of the sources of the Kyga, which enter the southern end of Lake Telets, the upper reaches of the tributaries of the Chulyshman—Chulcha and Shavla, the source of the Chulyshman itself—and the region of Lake Dzhuvlu-Kol' (Dzhulu-Kul') (Dmitriev, 1938; V.G. Heptner).[313] Evidently reindeer are encountered even slightly south

---

man. Evidently the occurrence of the animal was limited mainly to the eastern part of the Altai (see below) even in the remote past. Jacobi (1931), with a reference to Falk (1786), mentions the occurrence of reindeer "in the Kuznets mountains or Kholzuna to the north of the upper Irtysh", probably based on some misunderstanding. Falk simply mentions the Kuznets mountains, evidently having in mind the Kuznetsk Alatau. Jacobi, with a reference to Cochrane, also mentions the occurrence of reindeer in the Kalbinsk Altai, which is erroneous since reindeer were never present in these mountains.

[312] Boundary in western Siberia according to Yanushevich and Blagoveshchenskii (1952, map) and Druri (1949), with some modifications.

[313] The outlines of the range boundary in Altai shown in the map published by Yanushevich and Blagoveshchenskii (1952) differ sharply from those given above and do not correspond to the prevailing position. Evidently reindeer even in the past (see above) were not as extensively dispersed in the Altai as indicated in the map referred to above.

and southeast of the source of the Chulyshman, in the southwestern high-montane portion of the Tuva district, although there is no positive proof of this.

Farther east the boundary (reconstructed) runs along the Tannu-Ola range[314] (Radde, 1861; Middendorff, 1867; Jacobi, 1931; and Carruthers, 1911*), and into Mongolia.

At present the boundary in this section runs along the Sayans, and includes neither the southern nor the central portions of Tuva (Yanushevich, 1952). The range at present includes, however, the eastern Tuva uplands, especially the source region of the Bol'shoi and Malyi Yenisey adjoining Mongolia and probably the Sangilen mountain range.[315] Accurate data on the boundaries in this region are, however, inadequate (Kopylov, 1950; Yanushevich, 1952; and others).

Even farther east in the past as well as now, the range boundary and the state boundary occurred in the same region to the Okin range and the source of the Oka, in the Kitoi and Tunkin systems, 317 and still farther east extends into Dzunsk-Murin range and other mountains along the left bank of the Dzhida (Trans-Kamensk Aimak [Mongolian administrative unit]). Farther on the range covers all of Khamar-Daban (Kopylov, 1950; Favorskii, 1936; and others). No data are available on the occurrence of reindeer in the mountains on the right bank of the Dzhida (Dzhidin range) but the animal possibly occurred there in the past.

It is extremely difficult to establish the southern boundary of the range in the rest of Trans-Baikal. In the eighteenth century the animals probably covered all of the montane region, obviously being absent in steppes and in general, in open plains. The range encompassed all of the Yablonovyi range and even the Borshchovochnyi (Radde, 1862). Direct references are available to the occurrence of reindeer even in the expanse between the Shilka and Argun, probably in the northern and eastern parts of this interfluve region, and also along the Onon (Jacobi, 1931).[316]

Evidently from the northeastern part of the interfluve region or from the point of confluence of the Shilka and Argun, the range ran into Manchuria in the Great Khingan [mountains] (Pallas, 1811; Middendorff, 1867; Radde, 1862).

[314] Labeled Tangnu mountains by Middendorff (1867).

*Not in Literature Cited—Sci. Ed.

[315] This is evidently how the mention by Potanin (1881) of occurrence in eastern Tannu-Ola and in the Tes River basin (Bannikov, 1954) should be interpreted.

[316] The assumption of this author about occurrence in the Erman and Argun ranges can hardly be substantiated.

The southern boundary in Trans-Baikal underwent extensive and rapid alterations even at the commencement of the last century. By the middle of it there were no reindeer in the region between the Shilka and Argun (Radde, 1862). In the 1850's the range boundary, commencing at the source of the Onon at the state boundary, proceeded along the Borshchovochnyi range and intersected the Ingoda not far from its mouth. Farther on it turned along the Shilka or at some distance from it and ran to the point of confluence of the Shilka and Argun (reindeer were reported below Gorbitsa; Radde, 1862).

By that period the boundary had receded there also from the uppermost reaches of the Amur proper, which the animal had earlier occupied (i.e., rivers below the confluence of the Shilka and Argun). In the Amur valley itself reindeer "were evidently absent" in the 1850's. They were encountered "deep in the mountains" on both sides of the river, i.e., to the north as well as the south (Radde, 1862). Slightly later the boundary there evidently receded even farther. Thus, on the banks of rivers entering the Amur above Albazin reindeer were already absent in the 1860's and the boundary proceeded evidently into the region of 54° (Middendorff, 1867).[317]

In the last decade of the nineteenth century the boundary shifted still more slightly northward, although to a lesser extent than one would have anticipated. It encompassed Khamer-Daban, ran to the Yablonovyi range in the region of Chita or the divide between the Uda and the Vitim, and from there through the divide between the Chita and the Nercha, or through the lower course of the Nercha toward the source of the Olekma (Podarevskii, 1936; Favorskii, 1936; Druri, 1949; and others). i.e., roughly at 54°.[318]

Farther on the boundary ran along the Amur, which separates the Manchurian part of the range from the Siberian in this region, roughly up to the mouth of the Khumaerkhe River, entering the Amur from the right above the mouth of the Zeya (Radde, 1862). Evidently, it is there that the line marking the boundary of the Manchurian section of reindeer occurrence from the east intersected the Amur and entered the USSR. From there the boundary rose northward and later turned east, thus withdrawing from the Amur toward the mountains, encircling to the north the steppe-type expanse of the lower reaches of the Zeya and the Zeya-Bureya lowland. Apparently, it again approached the Amur in the Bureya mountains. Running farther again away from the river to the northeast and east, the boundary intersected the Amur roughly at 49° (probably more northward) and crossed into Sikhote-Alin. There the range descended in the form of a projection along the elevated portions of the mountain range down to 47° (Edel'shtein, 1906; cited from Jacobi, 1931). Later the boundary turned sharply north and ran toward the Tatar Strait at Sovets Gavan (Khadzhi) at 48° (Pallas, 1811; Middendorff, 1867; Radde, 1862; Schrenk, 1859; Jacobi, 1931; Maak, 1859; Druri, 1949; Abramov, 1954; and others).

---

[317] Albazin is slightly below the mouth of the Bol'shoi Never on the Amur (opposite the mouth of the Amuerkhe entering the Amur from the right). Middendorff referred to the rivers as Tepara and Liver but the latter should evidently be taken as the Never.

[318] Some researchers (Druri, 1949) point out that from the upper course of the Olekma the boundary "ran toward the Amur River above Albazin". As shown in the foregoing discussion, this information (its source not clearly known) is extremely outdated.

318 The boundary described above had undergone considerable changes at some places even by the middle of the last century. Around the Amur reindeer were absent and encountered only in the mountains to the north—in the Tukuringra range, the Bureya range away from the river, in the Turan and Vanda mountains, and so on.

In the recent period the boundary line coming from the west from the source of the Olekma intersected the source of the Ol'doi (around 55°) and later ran along the southern slopes of the Tukuringra range (around 54°20'; Gassovskii, 1927). In a manner not yet clearly understood, it extended farther away in the southeast somewhere along the mountains on the left bank of the Zeya and into the Bureya basin, intersecting this river roughly at 50°20'.

Farther on, descending slightly southeast, it encompassed the left tributary of the Bureya, i.e., the Tyrma, without, however, descending south of 50°. Turning almost straight east or rising slightly north, it later passed through the upper reaches of the Urma, intersected the Kur slightly north of 50° and ran toward the Amur slightly below the mouth of the Khungara (around 50°20'). Thus the boundary encompassed the Turan range, part of the Bureya range, and Badzhal' range. From the Amur it ran eastward to Sikhote-Alin, toward the upper reaches of the Khungara. From there it turned steeply south, and leaving the Anyui basin outside the range, encompassed the Tumnin and Koppa basins. Turning southeast it ran eastward to the sea at 48° or slightly north of 48° (Abramov, 1954; map).

From the outline of the range boundary of reindeer in the Amur region given above it may be seen that, over a century, it changed relatively little and less than at many other places in the range. Furthermore, it is highly possible that in the far remote past reindeer penetrated farther south in Sikhote-Alin than is known to us.

The range includes Sakhalin, reindeer having penetrated there to the southern extremity of the island, i.e., to 46° (Schrenk, 1859; A.M. Nikol'skii, 1889). This is the southernmost point of occurrence of reindeer in the USSR and in the Old World as a whole.

In the north the range everywhere reached up to the coast of the Arctic Ocean. It included not only small and large islands directly adjoining the mainland (for example, Nordenshelld [Nordenskiöld] archipelago, Bogicheva, Dikson [Dixon], Kil'din Islands, etc.) but also Solovetsk Islands, Kolguev (Lepekhin, 1805; Trevor-Bette, 1894), Vaigach, southern and northern islands of Novaya Zemlya, Belyi Island, southern island of Severnaya Zemlya (Ushakov, 1953), New Siberian Islands including Belkovskii, Kotelnyi, Zemlya Bunge [Bunge's Land], Fadeev, Novaya Sibir', and even Vil'kits and Bennett Islands, Medvezh'e, and especially Chetyre-khstolbovoi and Krestovskii Islands (Druri, 1949). In the Franz Josef archipelago, in the northern islands of Severnaya Zemlya and Wrangel Island reindeer were absent and never present, as also in small islands far away from the mainland (Uyedineniya Island).

The eastern boundary of reindeer distribution is represented by the coasts of the Bering and Okhotsk Seas. The islands of these seas, particularly the Shantar, do not fall in the range.

In addition to the changes in the southern boundary observed above, the range in the Asiatic part of the Soviet Union underwent extremely intense changes. Considerable gaps have been identified, which continue to enlarge, and at some places the northern and northeastern boundaries have undergone intense alteration. At the same time, because of scanty information and partly because of these very rapid alterations throughout the range, it is extremely difficult to chart an accurate map of all these fluctuations. Thus generalized notes are given here on the more significant and prominent changes.

At present reindeer are absent at most places along the railway line from Tomsk to Baikal. At some places they have withdrawn northward as well as south of the line for considerable distances. Thus the Altai-Sayan region of occurrence and its population of reindeer is becoming increasingly isolated from the central Siberian. This phenomenon is analogous to the isolation of the Karelian section of the range from the Ural section in the European part of the USSR. All this indicates an extensive destruction of the range.

In the northwest the northern boundary of the range, commencing from the southern extremity of Baydarat Bay, running east, 319 intersects Yamal [peninsula] roughly along 68°, and crossing the Tazov peninsula at the same latitude runs into the Yenisey. Inscribing a broad arc to the north on the right bank of the Yenisey, the boundary line, running west, intersects the southern part of Yenisey Gulf roughly at 70°. Farther on it cuts across the Mamont, Yavai, and northern part of the Yamal peninsulas slightly south of 72°. Reindeer occur north of this line but are absent south of it inside the "loop" formed by the boundary commencing at Baydaratskaya Bay (Druri, 1949).[319]

Reindeer are mostly absent throughout northeastern Siberia. The range boundary there runs from the Kolyma estuary along the Omolon into Gizhiga Bay (Sea of Okhotsk). Reindeer are also absent in northern Kamchatka north of the line Ust-Kamchatka-Lesnaya (Sea of Okhotsk). In this part of Siberia, there are probably two insignificant sections of reindeer occurrence isolated from each other and from the main Siberian range. One lies in the Anadyr mountain range north of Kresta Bay and the other in the region of the mouth of the Mayno in Anadyr (Druri, 1949).[320]

Geographic Range outside the Soviet Union

In the Scandinavian Peninsula the range (reconstructed) extended as a narrow irregular tongue along the highest mountain areas without, however, reaching the Atlantic coast. The range extended southward to southern Norway (58°40′) and reached the northern extremity of Lake Sudalsvatnet, 40 km short of the coast of the North Sea. On the Swedish (eastern) slope of the Scandinavian range the boundary ran away from the Baltic Sea (in the south particularly through Sern) and went around the Gulf of Bothnia on the north (Jacobi, 1931).

In Finland the range covered much of the country and reached in the west up to the Gulf of Bothnia. In the south it extended to Vaasa and the boundary passed along the northern extremity of the lake region (Jacobi, 1931). Judging from reindeer distribution within the USSR in the past, or even at present, one may assume that the range in the south reached 62° and perhaps even the Gulf of Finland in the remote past.

Ouside the Soviet Union the range also extended to Mongolia and northeastern China. In Mongolia it was limited to the northernmost part of the country in the region of Lake Kosogol (Hobsogol), which is closely associated with the Sayans and partly with Tannu-Ola. Probably reindeer in the past covered all of the expanse north of 50° and, maybe, a little more southwest to the source of the Tes River. At present reindeer are encountered only in some insignificant sections along the upper reaches of the right tributaries of the Tes River (southwestern Pri-Kosogol region), along the boundary with the Soviet Union in northwestern Pri-Kosogol in the montane part of eastern Tuva, and to the east of Kosogol in regions adjoining the Soviet Union at the source of the Uri-Gol (Bannikov, 1954).[321] It is quite possible that reindeer may have penetrated in the distant past from Trans-Baikal even into the northern outskirts of Khentei but these animals were absent there in the middle of the last century (Radde, 1862).

---

[319] According to the latest data reindeer are currently absent throughout Yamal and seen rarely only on the Belyi.

[320] This information pertains to the 1930's and much earlier and is probably no longer true.

In northeastern China reindeer occurred in the Great Khingan and also evidently the Ilchuri-Alin' [I-le-hu-li Shan] (Pallas, 1811; Radde, 1862; Jacobi, 1931). No details are available about the distribution of the animal there, but evidently they inhabited the northernmost part of the mountains.[322] This region was directly associated with the occurrence of reindeer in the USSR along upper Amur (see above). In northeastern China reindeer were long absent but did exist there even in the middle of the last century (Radde, 1862), disappearing from the region at the end of the century.

A large part of the range of reindeer, albeit much smaller than in
320 the Old World, lies in North America. In the west the major portion of the range earlier formed a large extension southward along the Rocky Mountains and also evidently the Cascade Range. The southern boundary there ran along the Columbia River or slightly more south in northern Oregon. Farther away it traversed roughly along 46° into Idaho and extended in the east to Fort Benton in Montana. From there, running to the west of the vast steppe areas of the Saskatchewan basin and the lowlands of the Athabasca River, the boundary ran along the eastern slopes of the mountains straight north and even inclined slightly westward. In the north it ran along the Peace River, commencing from its source in the Rocky Mountains, toward Lake Athabasca. From there it turned southeast toward Lake Wollaston and Reindeer Lake, intersected the Churchill River

---

[321] References to habitation in Kobdo region and in Changhe (Flerov, 1952) are erroneous. Radde (1862) made an extremely cautious statement about this for only part of the high mountains. Reindeer are absent in Changhe and were never present in the past (Bannikov, 1954).

[322] In the map given by Radde (1862) the extent of the range in the south is to 50°. Habitation in the Khan-Zol mountains of Manchuria has also been indicated (Pallas, 1811) (V.H.).

at Reindeer River, ran into the Saskatchewan River and to the eastern shore of Lake Winnipeg and Lake of the Woods. Farther on the boundary covered parts of Minnesota and Wisconsin adjoining Lake Superior. The range included at least the northern half of the peninsula between Lakes Michigan and Huron. More to the west, the boundary evidently ran along the shore of Lake Huron and later crossed to the St. Lawrence River. Along the banks of this river reindeer evidently were not found within New York State (Adirondack mountains in the north) but east of Lake Champlain the range encompassed Vermont and New Hampshire and even Massachusetts. There, roughly at 42°30′ lay the southernmost point of the habitation of reindeer in America and of the range in general (Jacobi, 1931; Burt, 1938).

The Atlantic and Pacific Oceans form the eastern and western boundaries of the range, but evidently the range boundary did not reach directly up to the Pacific Ocean coast in the south. The northern limits of the range on the continent were formed by the northern coast. The range included Newfoundland in the Atlantic Ocean, the Queen Charlotte Islands, Kodiak and Unimak* of the Aleutian Islands, and the entire Arctic archipelago.

In Greenland the region of reindeer distribution covered all of the coast except the extreme south of the western part of the island and the area south of Angmagssalik (slightly south of the arctic circle) in the east (Jacobi, 1931). Farther to the east the boundary bypassed Iceland and encompassed Spitsbergen. Later the boundary entered the USSR (see above).

The range of reindeer in America, compared with the foregoing, varied intensely. In general, the southern boundary everywhere withdrew intensely to the north leaving only some stray islands of habitation within the range on the mainland.

Domesticated reindeer existed only in the Old World. American native people did not know about domesticated reindeer and this animal was only an object of hunting for them. Domesticated reindeer were introduced in America only at the very end of the nineteenth century. At present they are abundant there.

Reindeer (domesticated) were introduced into several countries (Orkney Island, Great Britain, Denmark, Germany, Austrian Alps, Switzerland, Italy, and Latvia), but without success. In addition to America, acclimatization proved successful in Iceland and the islands of south Georgia (subantarctic). (V.H.)

---

*Given as "Univak" in Russian text—Sci. Ed.

Geographic Variation

The magnitude of geographic variation in the species as a whole in terms of morphological characteristics and number of forms is quite significant, but evidently less, especially in America, than usually assumed.

Geographic variation in reindeer of the Soviet Union has been studied repeatedly (Druri, 1949; Sokolov, 1937; especially Jacobi, 1931; Flerov, 1932, 1933, and 1952). Yet the schemes put forward, including the latest (Flerov, 1952), cannot be considered satisfactory. In fact, only one species has recently been proposed for the Soviet Union as a whole. However, characteristics of the races, their geographic ranges, taxonomy, and even their number, are not yet
321 clearly known. Insofar as the latter is concerned, the prevailing tendency is toward excessive division. Due to various factors the material available concerning this species in Soviet museums is extremely slim and its variability high. This is particularly true of individual and seasonal color variations.

A matter of considerable importance is the fact that domesticated animals and hybrids sometimes occur among wild reindeer and cannot always be distinguished. Some researchers describing reindeer races have not been aware of the foregoing facts, or sometimes deliberately base their observations on data for domesticated reindeer. Finally, even the nomenclature of this species is in a state of confusion. Hence the taxonomy of reindeer races given below should not be condidered definitive; further study is required for its improvement.

Geographic variability in reindeer of the Old World exhibits two major tendencies. One concerns size variability. Reindeer inhabiting islands and tundra of the Far North adjoining the Arctic Sea are smaller than those inhabiting the forest zone. The more southerly, the larger the animal; those on the coast of Okhotsk, in Sakhalin, and southern Siberian mountains are especially large. The ratio of body length of northern ("tundra") to forest ("taiga") reindeer is roughly 5 : 6, and the weight difference naturally much more.[323] Moreover, forest reindeer evidently have slightly longer legs, which should be regarded as an adaptation for the much deeper and softer snow in the taiga.

Variations in overall skull dimensions are as follows: mean maximum skull length of Novaya Zemlya reindeer 345 mm; tundra animals 368 mm; Siberian forest zone animals 382 mm; and reindeer of

---

[323] According to other data (Druri, 1949) almost double, which, of course, is an exaggeration.

Okhotsk coast 415 mm (Druri, 1949). Spitsbergen reindeer (*Rangifer tarandus platyrhynchus* Vrolik) are particularly small. Their small size is evidently the result of isolation on the island and island-type speciation. On the whole, trends in change of size in reindeer run contrary to Bergmann's rule. The direction is evidently determined not by thermal regulation but by other factors, probably the nature of the snow cover, which is more massive in the forest zone. Color changes also tend to exhibit a definite geographic gradient. Reindeer of the Far North are mostly light-colored and often almost or even totally white. Light coloration is a genetic property of northern animals and, moreover, discoloration and bleaching of fur proceed rather intensely in open tundra. Reindeer of the forest zone are generally dark, being darker than northern animals. Evidently the farther the distance southward, the greater the color intensity. Reindeer of the Okhotsk coast and Sakhalin are particularly dark. In spite of this, even in the south light-colored reindeer occur, which at places turn almost white by spring (Altai).[324]

Five subspecies are tentatively distinguished within the Soviet Union.[325]

1. European reindeer, *R. t. tarandus* Linnaeus, 1758 (syn. *rangifer, lapponum, guettardi, schottingi, furcifer, typicus, cylindricornis, fennicus,* and *silvicola*).

Small-sized.[326] Maximum skull length 335 to 400 mm (M 360). Color of winter coat relatively dark with well-defined light- (particularly on the sides) and dark-colored fields. Dark brown color of back stands out prominently from light coloration of upper part of neck. Brown longitudinal band from ulna to femur prominent.

322 Occur in the forest and tundra zones of the European part of the USSR, evidently excluding the Urals. Outside the Soviet Union found in Finland, Sweden, and Norway.

This form includes forest as well as tundra reindeer, which are usually placed under different subspecies throughout the rest of the species range. Attempts to distinguish forest reindeer of the Scandinavian Peninsula and forest zone of the European part of the USSR from those inhabiting mountain tundras in the Scandinavian Peninsula under the name *R. t. fennicus* have not been successful. This race has been very poorly studied and its relation to the Siberian forest form as also to Siberian tundra reindeer is not clear. Likewise the boundaries of distribution of this form are not precisely known. These questions have evidently to remain unsolved since this form has become totally extinct in the tundras and is becoming almost so in the forest zone.

---

[324] These two major tendencies in geographic variability are also seen in America where groups of forest and tundra reindeer are distinct. Along with extremely dark forms there are some which turn white in winter (*R. t. arcticus* from Mackenzie), and even some which are white in winter and summer as well (*R. t. pearyi,* Ellesmere Island, 79° N lat.). Large and small forms likewise exist. The geographic gradient of changes is similar to the corresponding Eurasian forms.

[325] Mainly according to data from Flerov, 1932, 1933, and 1952; Druri, 1949; Sokolov, 1937; Jacobi, 1931; and also based on original data by V.G. Heptner.

[326] Compared with races of Russian fauna, excluding Spitsbergen and American reindeer.

2. Novaya Zemlya reindeer, *R. t. pearsoni* Lydekker, 1902.

Rather small, generally corresponding to the nominal form or slightly smaller. Maximum skull length 319 to 375 mm (M 345). Skull slightly more narrow and extended. Color very light and winter fur almost totally white; only top of back, neck, and head, and sometimes even anterior part of the limbs a very light rusty-brown. Lateral band absent. Fur thicker, long, and dense; mane longer than in other Eurasian reindeer forms.

Occur in Novaya Zemlya. Not found outside the Soviet Union.

The relation of this form to the Siberian tundra form is not clearly known. Indubitably they are closely related; reindeer of this type of coloration are found in Yamal and other regions of Siberian tundras. Novaya Zemlya reindeer represent a somewhat extreme variety of this type, and have a restricted geographic distribution, thus justifying their separation. They are quite analogous to some American Arctic forms (*R. t. arcticus* or *pearyi*).

3. Siberian tundra reindeer, *R. t. sibiricus* Murray, 1886 (syn. *lenensis* and *asiaticus*).

Dimensions somewhat greater than those of nominal form. Maximum skull length 346 to 420 mm (M 373). Color of winter coat very light and similar to that of Novaya Zemlya form. Dark patches in general equally pale but dark band on side distinct though light in color. Fur very dense and long. Skull comparable to that of nominal form but with slightly more elongated rostral region.

Found in Siberian tundras and Arctic Ocean islands along Siberian coast. In Anadyr region they are dispersed southward up to 60° N lat. During winter migration they occupy even the northern outskirts of the taiga. It is quite possible that tundra reindeer of northeastern sector of the European part of the USSR also belong to this form. This form does not occur outside the USSR.

Forms in eastern and western tundra zones are possibly not identical. Reindeer of northeastern Siberia are evidently close to those of Alaska.

4. Siberian forest reindeer, *R. t. valentinae* Flerov, 1933 (syn. *angustirostris*).

Moderate size but somewhat larger than tundra animals. Maximum skull length 355 to 404 mm (M 382).[327] Color of winter coat "light rusty-brown or sandy-brown. Pure white color present only on abdomen, inner sides of limbs, lower part of neck, on very small speculum, and lower part of tail. Dark color of back not distinctly set off and blends very imperceptibly into light color of neck and shoulders. In general, all dark- and light-colored patches not distinctly demarcated as in typical Lapland reindeer, but gradually blend into each other. Top of head darker in color than back. Longitudinal bands on sides of trunk highly distinct. Fur significantly shorter than in tundra and Novaya Zemlya reindeer, approaching
323 coat of *R. t. tarandus*" (Flerov, 1952). At some places in high mountains the winter fur evidently fades by spring to almost total white (pointed out for Altai; F.D. Shaposhnikov, 1955).

At some places (Altai) some sexual dimorphism in color is also discernible. The light-colored lateral band and light-colored neck in males is much sharper than in females.

It is significant that in the Altai and Sayans females often have very weak and thin, sometimes unbranched, antlers, and up to 25 to 33% are devoid of antlers.[328] In the rest of the range of the species hornless females are a rarity.

This form occurs in the forest zone of Siberia in the east up to the Stanovoi range and Dzhugdzhur, the south Siberian mountains to the Altai in the west, and the Urals. Outside the Soviet Union found in northern Mongolia. The distribution boundaries of this form in relation to the next one are not yet clearly known; its geographic differentiation from the European form remains particularly elusive. It is possible that the Siberian form reached the Volga (in Tatariya, see above).

A distinct species of reindeer, *R angustirostris* Flerov, was described from the Barguzin range. It is characterized by a narrow facial portion of the skull (Flerov, 1932). Later (1952), Flerov transferred this form to a subspecies. In fact, however, the difference is evidently no greater than individual variability among Siberian forest reindeer. This is emphasized since, as pointed out by Flerov (1935), it coexists with Siberian forest reindeer (*R. t. valentinae*).

---

[327] For more details of measurements of some Altai reindeer see F.D. Shaposhnikov (1955).

[328] Sometimes this is considered a primitive characteristic and the population in these regions dubbed "relict" (Mashkovtsev, 1940; F.D. Shaposhnikov, 1955). The question requires further study since the percentage of hornless females (sometimes reported as even up to 50%) has been established largely through questionnaires and visual observations, the factual (collected) material being very little. Visual observations could create false impressions, especially while observing herds, because bulls and adult females (barren and fawned) shed their antlers at different times.

Note: The synonyms of Siberian reindeer are not yet clearly understood but evidently the name *valentinae* cannot be supported. From among the names given by Millais in 1915, the names *chukchensis* and *jakutskensis* pertain to domesticated forms and have no nomenclatural significance. The name *buskensis* evidently refers to the wild form but was rejected by K.K. Flerov (1935) without substantiation. In fact, there are neither reindeer nor "Busksk mountains" near Semipalatinsk. Nevertheless, there is every reason to presume that Altai reindeer were received from Semipalatinsk. It is similarly possible that the word "Busk" (written Besk) is a distortion of "Biisk"; in other words, the reference is to reindeer "from the Biya mountains near Semipalatinsk." However strange such a geographic identification sounds to us at present, it was quite natural for foreign hunter-sportsmen at the beginning of this century. The rest of the arguments for rejecting the name *buskensis* are also not well founded. According to K.K. Flerov (loc. cit.) there were no reindeer after 1907 in Altai, and hence Millais could not have obtained material from there. But reindeer were present at Altai then and are present even now. This cannot be a reference to "Airat" (i.e., Oirot) domesticated reindeer since Oirots do not raise reindeer. Apparently the correct name for Siberian forest reindeer should be *R. t. buskensis* Millais, 1915 and *valentinae* placed as a synonym. In both forms even the typical habitats coincide. The name *valentinae* is retained tentatively for want of a more detailed analysis of the question.

5. Okhotsk reindeer, *R. t. phylarchus* Hollister, 1912 (syn. *setoni*).

Largest of all reindeer occurring in the Old World. Skull large and massive, with a maximum length of 392 to 438 mm M 415). Color of winter coat similar to that of nominal (European) form, but darker. Dark color on back extends forward to a greater extent and encompasses nape. Lateral dark band distinct. Often abdomen also dark-colored and light-colored region on sides small. Profile of facial region of skull more convex than in other forms.

This form is found in Kamchatka, regions adjoining the Sea of Okhotsk (Dzhugdzhur range), Amur region, including southern spurs of the Stanovoi range, north Ussuri region (Sikhote-Alin range), and Sakhalin. It has not been mentioned outside the Soviet
324 Union but it is possible that the range included the northern part of the Great Khingan and probably Little Hingan [mountains]. At present reindeer are evidently absent in these mountains.

The Okhotsk reindeer is a well characterized form but with some paradoxical distribution: not only Sakhalin but evidently also the Kamchatka part of the range is discontinuous from the mainland part of the range. According to some data (Flerov, 1952) the range of tundra reindeer (*R. t. sibiricus*) in northeastern Siberia (in the Anadyr region) descends in the south up to 60° N lat.

* * *

In North America and Greenland geographic variability of reindeer is very distinct. Although it has been studied several times, information is still wanting. Some American authors (Miller and Kellogg, 1955) have acknowledged three species to date for North America (*R. arcticus, R. pearyi,* and *R. caribou*) with 15 races. This scheme is unsatisfactory. There are no new species in America and no more than eight geographic races of *R. tarandus* there.

Recently (Haltenorth and Trenze, 1956) have acknowledged eight races: *R. t. groenlandicus* Bor., 1780 (Greenland), *R. t. pearyi* J. All., 1902 (islands of American Arctic archipelago), *R. t. arcticus* Rich., 1829 (tundra west of Hudson Bay including Alaska), *R. t. caboti* G. All., 1914 (Labrador and northern Quebec), *R. t. terraenovae* Bangs, 1896 (Newfoundland), *R. t. caribou* Gm., 1788 (central region of America from southern Quebec to Great Bear Lake), *R. t. montanus* Th.-Set., 1899 (montane regions from northern Idaho up to southern Yukon), and *R. t. dawsoni* Th.-Set., 1900 (Queen Charlotte Islands). Some of these forms stand out prominently while others are dubious. It is quite likely that their actual number is less. (V.H.)

Biology

Population. The most significant stocks of wild reindeer are in Taimyr, in the region of the Lena delta, and in the Yana-Indigirka tundras: altogether their population in all three regions could be placed roughly at 250,000 to 300,000. In the rest of the range, which in area is several times more extensive, the population of wild reindeer does not exceed 100,000 animals.[329] A century ago the number of wild reindeer in the Soviet Union was evidently reckoned in millions but since then decreased 10 to 15 times. There is no doubt that in the very remote past, when the range of wild reindeer was incomparably more extensive, their population was even greater.

---

[329] According to the computations of Terletskii (1932), based on the data of polar records for 1926 to 1927, about 400,000 wild reindeer lived in the regions of the Far North of the USSR in those years. These figures are evidently underestimates for those years since they, in turn, were based on clearly underestimated data on the extent of wild reindeer catches.

The population reduction of wild reindeer intensified considerably from the end of the nineteenth to the early twentieth century, but this process has become particularly intense since the 1930's because human settlements in the northern outskirts of Siberia have multiplied rapidly. Besides direct extermination a great role is played by [domestic] reindeer herders in crowding wild reindeer into areas less favorable to their mode of life, severe trampling of mosses by herds of domesticated reindeer, and the total destruction (by fires and felling of forests accompanied by the destruction of moss cover and arboreal lichens) of the main habitats of wild reindeer. As a result, it is extremely significant that populations of domesticated and wild reindeer are found in inverse ratios: at places where the former abound, the latter are few. Interesting data on this subject are available in polar records for 1926 to 1927, also in Terletskii's work (1932), and particularly in Druri's (1949).

Right up to the early twentieth century wild reindeer were fairly common on both of the main islands of Novaya Zemlya in which
325 they lived year-round. At the end of September, 1832 in the southeastern extremity of Novaya Zemlya at Kamenka Bay, Pakhtusov (1842) saw a herd of wild reindeer numbering roughly 500 animals. At the end of the nineteenth century there were over 20,000 reindeer on both islands, decreasing to only a little over 1,000 by the 1930's and dwindling to only several dozen in the 1950's (Zubkov, 1935; Uspenskii, 1958).

Reindeer were numerous on the New Siberian Islands. At the end of the 1920's there were 7,000 to 8,000 on Bol'shoi Lyakhovskiy Island; 4,000 to 5,000 on Novaya Sibirsk Island before their epizootic loss in 1924; and several dozen to a hundred in the rest of the islands. In winter most of the animals migrate to the mainland (Pinegin, 1932). As a result of the formation of glaze ice in 1924 and 1935 and intensive hunting, the population of New Siberian wild reindeer had shrunk by the end of the 1930's to several dozen or, at best a hundred animals (Skalon, 1940; and others).

In 1929 the entire population of wild reindeer on Yamal was placed at 8,000, most of which went over to Belyi Island in summer. In the summer of 1930 there were about 5,000 wild reindeer on Belyi, but only 2,179 in the autumn of 1935; several hundred remained on the island to winter and the rest wandered onto the mainland (Tyulin, 1938). Subsequently the reindeer population on Belyi Island shrank drastically so that by 1949 no more than 300 animals were counted there (Uspenskii, 1949). In the mid-1930's on Bogicheva Island (eastern Taimyr) there were 2,000 to 2,500 reindeer in summer but only a few remained to winter (Koshkin, 1936 and 1937). In the remaining polar islands only several dozen or a hundred reindeer were found. At present wild reindeer are few in all the polar islands. Their number is usually insignificant in the islands of the Soviet Arctic region.

Wild reindeer are also few over a considerable expanse of Sakhalin (more common from Schmidt Peninsula to Terpniya Bay and also in the region of the former Central Sakhalin preserve; Mishin, 1952; E.P. Volkova). In the nineteenth century wild reindeer were abundant on Sakhalin.

By the end of the 1920's the only place on the Kola Peninsula where wild reindeer still existed was the territory in which the Lapland preserve had been established. By the early 1940's the reindeer population in that region approached a thousand (in 1940 there were 942 animals, which by the next year increased to 970). During World War II shooting of reindeer was permitted in the preserve and a greater number were frightened away. The population declined notably but is gradually being restored (in 1951 there were over 500). Nowadays wild reindeer are also present in other regions of the Kola Peninsula, for example Ponoy basin. Most probably originated from domesticated animals lost during the war years. Others no doubt fled from the preserve in those years.[330] In the first half of the nineteenth century the reindeer population of the Kola Peninsula was much greater. In the basin of Lake Imandra a herd 300 to 400 strong was observed in winter (Pleske, 1887); during the latter half of the nineteenth and early twentieth century wild reindeer were abundant in Ponoy basin also (Charnolusskii, 1930).

In the tundras of the European part of the USSR (Bol'shezemel' and others) wild reindeer disappeared totally a long time ago (Sdobnikov, 1935; Druri, 1949). They were probably preserved in the Polar Urals but in negligible numbers (Uspenskii, 1958). Within the southern tundras of the Yamal, Taz, and Gydan Peninsulas, reindeer stocks were destroyed over 30 years ago and reindeer are few there even now. In the Yamal and Gydan Peninsulas they are preserved only in the northern parts and the distance between tundra and forest populations is 4 to 5°; in Malyi Yamal wild reindeer are absent (Dubrovskii, 1940; Druri, 1949; and others).

---

[330] Not from the forward [battle] regions as assumed by Druri (1949), since wild reindeer were absent in those years west of Murmansk railway station.

Wild reindeer are preserved in large numbers in the Taimyr, especially in the eastern part of the peninsula. The main places of
326 summer congregation do not fall south of 74° and extend north almost up to Cape Chelyuskin. In winter the majority migrate from the Taimyr tundra and congregate in the mountainous regions along the watersheds of the Dudypta, Kheta, Khatanga, Popigay, Anabar, and Olen'ok Rivers (Fig. 109), mainly in the region of forest-tundras and northern taiga.

Places of summer concentration of reindeer in the tundras of the Lena delta and adjoining regions are situated north of 71 to 72° N lat. Most reindeer of the western parts of the Lena delta migrate in winter to the divide of the Olen'ok and Anabar; many animals winter in the basin of the Dzhalinda River, a tributary of the Anabar on its right bank. Reindeer of the eastern regions of the Lena delta migrate in winter along the Kharaulakh range, and are distributed in the southern forest zone roughly to 67–68° N lat. (Skalon et al., 1941; Druri, 1949). Half a century ago wild reindeer were far more numerous in the Lena tundras.

East of the Lena, including the Yana delta, wild reindeer occur in tundras everywhere. Furthermore, according to the latest data (S.P. Naumov), their number is considerable at places; more to the east, roughly from the Khroma to the Indigirka, they are quite abundant. In summer reindeer occur mostly north of 70°; the main places of concentration are the Khroma basin and lowlands on the left bank of the Indigirka. In winter reindeer migrate into the mountains between the Yana and Indigirka, in particular into the Tas-Khayakhtakh range, east of the Indigirka on the Alazeya plateau, and in Mom' mountains, and to the south almost up to 66° N lat. (Fig. 109). In the mid-1930's the population of wild reindeer in the tundras of the Khroma and Indigirka was estimated at 150,000 (Mikhel', 1937).

Wild reindeer are few from the right bank of the Indigirka and farther eastward (basin of the Alazeya River and tundras in the lower reaches of the Kolyma and its tributaries). In the past the lower reaches of the Kolyma and Alazeya tundra were famous as one of the places where wild reindeer were most abundant in eastern Siberia. Seasonal migrations during which reindeer moved in herds of several thousands were particularly famous. Wrangel (1841) in describing autumn migrations across the tributary on the right bank of the Kolyma, i.e., the Malyi Anyui, writes that in some years the herds extended over "50–100 versts."* In 1847 no less than 70,000 reindeer crossed the Malyi Anyui (Argentov, 1860). Reindeer in large numbers moved into the lower course of the Kolyma even in the autumn of 1905 (Buturlin, 1913).

---

*Verst = 3,500 feet—General Editor.

On the Chukchi Peninsula and in the Anadyr basin, wild reindeer are very rare at present. In the nineteenth century they occurred, particularly in the Anadyr basin, in large numbers (Portenko, 1941; Druri, 1949).

In taiga and montane taiga regions wild reindeer are few and their distribution there at present is sporadic; wild animals are altogether absent at places where reindeer husbandry is well developed. In the past their numbers in the taiga parts of the range were considerable and they were common in the European part of the USSR also. However their numbers per unit of area, compared with the corresponding figures in summer in tundras, were significantly lower.

In the forest regions of the European part of the USSR wild reindeer subsisted in the Karelian Autonomous Soviet Socialist Republic, Komi Autonomous Soviet Socialist Republic, and in certain districts (Arkhangel'sk, Vologda, Perm, Kirov, and others), but their populations were not high. In the Komi Autonomous Soviet Socialist Republic, according to Ostroumov (1949), they were relatively more numerous in Ust-Tsilem, Udor, Kozhvin, and Troitsk-Pechora regions (on the territory of the Pechora-Ilych preserve 900 to 1,200 wild reindeer were counted at the end of the 1930's; Teplov and Teplov, 1947). In the Polar Urals, in the north of the taiga zone, wild reindeer were fewer than elk (Kurazhskovskii, 1949). They were also few in the northern Urals (Druri, 1949). They are still conserved in the northernmost part of the central Urals but extremely rare and evidently include domesticated reindeer turned feral (Ivdel' region).

In the north of western Siberia the wild reindeer population is not high, but in the basins of the Konda and Sosva, at least up to 1951, they were numerous and encountered in large herds (V.N. Skalon). In the interfluve regions of the Ob', Irtysh, and Yenisey, 327 reindeer were preserved only in small numbers and that not everywhere; for example, they became extinct quite long ago in the Vakhsh basin and have disappeared in the upper reaches of the Taz (Skalon, 1931).

In the basins of the middle and lower Yenisey there were three main regions of high concentrations of wild reindeer: the watersheds of the Angara and Podkamennaya Tunguska; Podkamennaya and Nizhnyaya Tunguska; and Nizhnyaya Tunguska, Vilyuysk, Kotuya, and Kureika (most of all in the latter region) (N. Naumov, 1930 and 1934). Over the last thirty years the wild reindeer population in the

Yenisey basin has decreased considerably. In the taiga regions of Yakutia (excluding the extreme north where a large number of reindeer come from tundras to winter), wild reindeer are few; in the central parts of Yakutia (midcourse of the Lena River and others), wild reindeer have not survived (Belyk, 1948 and 1953). In much of the northern and central regions of the Irkutsk district reindeer are also few but have survived in significant numbers in the Patom highlands (Skalon, 1951; and others).

In the Far East wild reindeer are relatively common in the upper course of the Bureya and its tributaries, the Akishma and Amgun (quite recently, a herd of 50 to 60 animals was sighted there), and in the marshy lowlands near Lake Evoron in the basin of the Gorin River; the range is broken up into several segments (Abramov, 1954). On the coast of the Tartar Strait and Sea of Okhotsk reindeer are currently few and totally absent at places; formerly, these animals were abundant. Until recently wild reindeer were also numerous in Kronots preserve (eastern Kamchatka), where their total population possibly reached 10,000 (up to 2,000 reindeer gathered in some wintering sites; Averin, 1948). After 1951 wild reindeer rapidly declined. In the remaining regions of Kamchatka they are few.

Small numbers of wild reindeer subsisted in the mountain systems of southern Siberia. At the end of the 1940's in the mountains

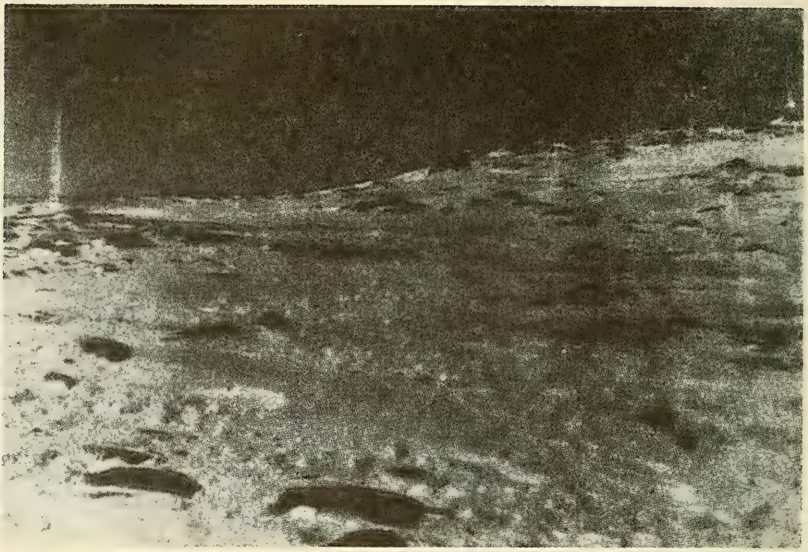
327 Fig. 104. Frightened wild reindeer herd. Source of the Chuzik River. Vasyugan'e. January, 1957. Photograph by K.T. Yurlov.

of the eastern Altai there were only 150 to 200 wild animals in an area of over a million hectares (Shaposhnikov, 1955). In Sayan preserve reindeer were evidently more common than in the Altai (K.M. Gromov). Reindeer were few in the Kuznetsk Alatau (Zharov, 1958). Several hundred wild reindeer have survived in the Khamar-Daban and the Ulan-Burgasy ranges (Fetisov, 1955).

Habitat. Reindeer are distributed in tundra (in the Arctic island at places represented by associations transitional to Arctic [polar] deserts), forest-tundra, and in the subzone of taiga forests; they do not emerge outside the latter into the zone of mixed forests. These animals are equally well adapted to living in plains and montane environs; they are sometimes seen at heights of over 2,500 m (Altai and Sayans) and do not avoid relatively steep slopes (up to 25 to 30°). In a considerable stretch of the range the optimum living conditions for reindeer are evidently found in tundra (in summer), forest-tundra, and montane regions, but the prevailing distribution of sites in which reindeer concentrate provides little data for an objective assessment of this subject, since it depends largely on human factors. Nevertheless, in dense taiga massifs reindeer have always been few, apparently; animals are found there mainly along the periphery and at places where dense forests grades into thin coniferous forests and extensive marshes. Reindeer penetrate genuine dense coniferous forests mainly in winter in search of food (arboreal lichens), for shelter from unfavorable weather conditions, and to hide from man even in relatively less populated localities (for example, southwest part of the range).

Thus in the taiga zone of the Soviet Union wild reindeer are mainly drawn to forest-tundra types of terrain. The same is largely true of the reindeer distribution in some montane regions where large numbers collect on bald hill tops and the upper portions of the forest belt with sparse tree vegetation (Shaposhnikov, 1955). The attraction of reindeer to relatively open terrain is one of the most characteristic features of their ecology (Naumov, 1934; Averin, 1948; Semenov-Tyan-Shanskii, 1948).

Reindeer inhabit temperate and cold climates. In summer they mostly prefer places where the heat is less, winds blow, and blood-sucking flies fewer. The availability of food and the possibility of shelter from predators are paramount in winter. However, all these factors often are of secondary importance compared to those caused by human activity (for example, herd distribution pattern of domes-
329 ticated deer). In summer and early autumn in the north of the mainland tundra adjoining the sea coast (for example, Taimyr) and also in the Arctic islands, wild reindeer are confined to lowland sections,



328 Fig. 105. Site of reindeer feeding in montane tundra. Lapland preserve. April, 1951. Photograph by O.I. Semenov-Tyan-Shanskii.

river valleys, depressions and swampy depressions with abundant herbaceous vegetation (grasses, sedge, and cotton grass). Close to sea coasts they often visit low coastal tundras wherever succulent herbaceous vegetation grows on saline soils (Sdobnikov, 1939). On the southern island of Novaya Zemlya, Gusinaya Zemlya (Aleksandrova, 1935), marshy sections containing a significant amount of cotton grass and *Dupontia fischeri,* and hummocky tundras relatively rich in grasses and shrubs, are of particular importance to wild reindeer in summer.[331]

In the tundra zone and in the Arctic islands (Belyi, Bogicheva, Bol'shoi Lyakhov, and others) reindeer feed in winter along the peaks and slopes of uplands, selecting the least snowy pastures. Their main food is not so much lichens (consumed in significant quantity only in early winter because of lesser accessible later due to deep, dense snow) as grasses and sedges (Pinegin, 1932; Koshkin, 1937; Tyulin, 1938; Shastin, 1939; and others).

On the Kara [Sea] side of the southern island of Novaya Zemlya, where a maximum number of wild reindeer wintered in the past, the animals were confined to the slopes and ridges of montane uplands

---

[331] These observations were made while studying the grazing grounds of domesticated reindeer imported in the 1930's into Novaya Zemlya. Aleksandrova's data are nonetheless applicable to wild reindeer.

(Zubkov, 1935). In Gusinaya Zemlya the peaks and upper parts of slopes of uplands covered with hummocky tundras are quite accessible for reindeer feeding throughout the winter. The snow cover there usually does not exceed 30 cm in height, with an average near 15 cm (winter of 1932 to 1933). In such pasturing grounds terrestrial lichens cover an average of only 0.4% and vegetation as a whole covers slightly less than 50% (including more than one-half mosses). Moreover, in late autumn and the first half of winter, until December inclusive, reindeer can graze on some marshes and also on more edible types of vegetation growing on hummocky tundras (30 to 40% covered with terrestrial lichens) on the gentle slopes of elevations and plateaus. Increasing snow depth renders these pastures less accessible to reindeer later (Aleksandrova, 1937).[332]

In southern tundra and forest-tundra where pastures are considerably richer in food (when not trampled by domesticated reindeer), wild reindeer often feed in summer not only in river valleys, but also on the slopes of uplands, all the more so since blood-sucking flies are far fewer there. Reindeer do not like monotonously uniform stretches of tundra, preferring areas with creeks, lakes, shrub thickets, especially willow, and small forest clearings (Sdobnikov, 1939).

In winter most reindeer move far south—away from tundra—into forest-tundra and northern taiga. A particularly large number of reindeer winter along slopes of mountain ranges, often above timber line, on balds and lichen-rich pastures. The restriction of wintering sites of tundra reindeer to balds in the forest zone is particularly characteristic of the interfluve zone of the Yenisey and Khatanga, and in the past also of the Anadyr basin (reindeer there are almost extinct and their mass wanderings have ceased). These subarctic sections are known for their great snowiness. But even in the region of the Verkhoyansk range where there is not much snow, a significant number of tundra reindeer climb up in winter onto balds (Nasimovich, 1955).

The seasonal way of life of reindeer has been traced best in Lapland (Semenov-Tyan-Shanskii, 1948; and others) and Kronots (Averin, 1948) preserves, i.e., in the northernmost taiga subzones in the subarctic. Both regions are characterized by montane relief but the altitudinal range in Kamchatka is significantly greater. In both preserves reindeer are extensively distributed in summer throughout the entire territory; in Kronots preserve from the sea coast to forest-
330 free high mountains (often up to 2,300 m), and in Lapland from the

---

[332] See preceding footnote.

banks of large lakes (lowest part of the preserve) to mountain peaks (about 1,000 m). In Kronots preserve the maximum number of reindeer congregate in summer in the hills at a height of 700 to 1,200 m, mainly in the broad upper courses of valleys—among glaciers and snowfields on meadows in the zones of (alpine) balds—departing only late in autumn when snowfall is heavy. In Lapland preserve the summer distribution of reindeer is more diffuse than in Kronots, comprising various forests, burned-over sections, banks of reservoirs, and heights above timberline. In July–August, warm months, a large number of reindeer are seen in upper parts of mountain-tundra pastures close to small snowfields, water sources, in highly shaded sections of the topography, and also close to mountain ridges, i.e., places where blood-sucking flies are few.

In Kronots preserve the maximum number of reindeer congregate in winter along windblown sections in the mountains at elevations of 700 to 800 to 1,200 to 1,300 m, places covered with lichens, and in herb-shrub pastures. Some animals winter in coastal lowland tundras but move away from them even in winters of normal snows in December–February into montane sites for wintering. In winters with little snow some animals winter in sparse deciduous forests. Reindeer leave montane pastures in spring (April–May), wandering into the forest and into coastal tundra, where they remain until the commencement of summer, after which they again climb en masse into the mountains.

In Lapland preserve reindeer are confined in the first half of winter to the forest zone (in the forest and along swamps) and more rarely to montane tundra, where they choose pastures which are relatively rich in lichens. In the latter half of winter most congregate in mountain tundras, generally at heights of 400 to 600 m. By selecting the least snowy pastures, reindeer are compelled to feed on
331 sparse reindeer mosses and in rocky Cetraria-poor tundra sections; there is far too much snow at that time in sections rich in reindeer moss.

Over an enormous expanse of taiga forests reindeer live in summer close to extensive bogs (sphagnum and others), in burned-over sections, sparse coniferous forests, going out onto previously mentioned meadows; in winter they concentrate in quite small areas: around marshes (often overgrown with sparse forest), in mixed pine groves rich in reindeer moss, and sometimes in dark coniferous forests abundant in arboreal lichens. Winter residence of reindeer in dark coniferous forests is particularly characteristic of the southwestern range (Komi Autonomous Soviet Socialist Republic, Perm and Kirov districts; also, in the past, Sverdlovsk district and

330 Fig. 106. Place of pasturing of wild reindeer and their tracks. Some reindeer pricked up their ears and some began running on being frightened by the sound of the airplane. Eastern part of Kola Peninsula. April, 1958. Photograph by A.B. Vasil'ev.

the former Kazan province) (Eversmann, 1850; Bogdanov, 1871; Sabaneev, 1872; Galin, 1881; Lobachev, 1930; Teplov and Teplov, 1947).

At places where there are watersheds in the uplands, reindeer often visit them in summer when blood-sucking flies are numerous elsewhere; if the lichen pasture there is a relatively less snowy, many reindeer spend the winter there. In the middle part of the Yenisey basin, possibly because of the deep snow of pasture land on the divides, reindeer descend in winter along river valleys into the forest (Naumov, 1934).

In most mountain-taiga regions the main places of summer concentrations of reindeer are usually associated with balds and the upper part of the forest belt in the mountains (Altai and Sayans, 1,500 m and above). Reindeer are relatively few in the forest in summer. However, in the northern Urals, and some areas in Siberia, especially in places where mountain pasture lands are preempted in summer by domesticated reindeer breeders, wild animals are not found in such places at that time of year. Wintering sites of wild reindeer in montane taiga regions, depending on the abundance of food and its accessibility, availability of escape cover from predators, presence of domesticated reindeer herds, and so on, are likewise located by and large near balds and in the forest close to its upper boundary (in inclement weather, they take cover in the forest), or in pine groves in the montane forest belt covered with reindeer moss, or around marshes, and very rarely in dark coniferous forest. Occasionally reindeer move to balds only in the latter half of winter, when the snow cover in the forest reaches 40 to 50 cm in depth. Reindeer descend into forests if glaze ice forms in mountain pastures.

The forest type of wintering site is particularly characteristic of those parts of eastern Siberia with little snow (Druri, 1949), while the montane type is typical of regions in southern Siberia with abundant snow (Altai, Sayans, and Barguzin range). However, even in regions of heavy snow some animals winter in sites of the forest type. The extreme adaptability of reindeer to type of wintering site can be judged from the example of Sakhalin, where they have been observed in winter in lowland lichen tundras in the northwestern part of the island, on extensive swamps in the Poronayask valley, in spruce-fir forests of the uplands, and on balds and in sparse forests on the eastern mountain range (Nikol'skii, 1889; Mishin, 1952; E.P. Volkov; and others). Some differences in selection of habitats by males and females have been noted, but this phenomenon by and large is manifested far less distinctly in reindeer than in red deer and some other ungulates.

Food. The species composition of plants consumed by wild reindeer has been studied very little. The information available is restricted to a few areas in the range and hence is incomplete. In Altai preserve about 100 species of plants have been identified as food of wild reindeer (F.D. Shaposhnikov, 1955); some are evidently occasional and consumed along with other food.[333] A list of 42 species[334] has been published for Lapland preserve; of these 13 have been confirmed from observations on free-grazing domesticated reindeer (Semenov-Tyan-Shanskii, 1948). In Khamar-Daban and Ulan-Burgasa mountain ranges no less than 37 species of plants have been recorded as food of wild reindeer (Fetisov, 1955). Information for other regions is more scarce and less reliable; authors do not always distinguish observations on feeding of wild versus domesticated reindeer

---

[333] Shaposhnikov lists 32 plant species as primary, 28 as secondary, and 12 tertiary in importance; the status of 26 species (including 8 varieties of mosses) is not yet known.

[334] No more than ten are common to the list compiled for Altai preserve.

332 (Abramov, 1954; and others) and lists of food plants of wild animals usually contain only a few additional species. On the whole in the USSR, 120 to 130 species of plants have been established as food utilized by wild reindeer.

For the northern (not south of 65° N lat.) regions of the USSR, i.e., covering only a part of the reindeer range, 318 plant species have been named as consumed by domesticated reindeer (Aleksandrova, 1940). There are only a few species of higher (vascular) plants which are either not consumed at all or barely touched by reindeer. These data point to the extreme diversity of food consumed by reindeer and without doubt the variety of plants utilized is far greater than known at the present time. Yet complete sufficiency among the foods of wild reindeer and their domesticated cousins is not possible. Left to pasture in some restricted regions, often at places where food has been greatly damaged by trampling, the animals perforce consume plant varieties not normally included in their diet. Obviously, much of the data on the feeding habits of domesticated reindeer are applicable to wild reindeer also.

The winter diet of reindeer is far less diverse than that of summer; the varieties of plants selected in winter are 2.5 to 4.0 times fewer than in summer. In this period of the year the rumen reveals increasing amounts of different varieties of plants, the food value of which is extremely low or nil. In Lapland preserve of the 42 plant species known to be consumed by reindeer, only 13 are consumed in winter (Semenov-Tyan-Shanskii, 1948); the corresponding figures for Altai preserve are 26 out of 98 (Shaposhnikov, 1955).

In summer reindeer are extremely discriminating in their choice of food and usually consume only those plants passing through the phase of leafing, shoot formation, and flowering, nibbling only the tender parts (individual leaflets, tops of uncoarsened stalks, flowers, and the whole racemes of willow herb [fireweed]). In winter, because the variety of available plants is limited and accessibility poor, selectivity is perforce curtailed and some plants utilized more completely (Aleksandrova, 1940; Semenov-Tyan-Shanskii, 1948; Druri, 1949). Foraging reindeer in winter remain longer at one place and do not wander as in summer picking up food here and there. Foliose lichens are consumed more fully in winter than in summer. Reindeer exhibit a distinct seasonal cycle in the consumption of many foods, but consume terrestrial lichens with considerable constancy throughout the year. It is known that an overwhelming majority of the world's ungulates do not consume lichens at all. Some Russian species of ungulates do consume them (mainly epiphytic), but usually only in winter and that too only in an insignificant quantity except for mountain sheep and musk deer. In the case of reindeer, however, lichens represent the main food in terms of bulk for most of the year and over a considerable stretch of the range; their importance drops notably only during the 2.5 to 3.0 months of summer.[335] However, in the rumen of two wild reindeer caught in Altai even in July and mid-August lichens constituted 45.8 to 74.5% by weight of the total food mass (F.D. Shaposhnikov, 1955).

Lichens are rich in carbohydrates with a high starch value; they are readily digested and assimilated by reindeer. They are poor in proteins and mineral matter (calcium and phosphorus); some are exceptionally rich in organic acids. Prolonged feeding predominantly on lichens often leads to a disturbance in normal metabolism and weight loss. Experiments with domesticated reindeer have shown that the nitrogen balance became negative when reindeer were fed exclusively on lichens; the body excreted more nitrogen by oxidation of body proteins than it received through food (Aleksandrova, 1940). Thus lichens alone cannot be significant even as maintenance food. 333 Together with green fodder, however, the importance of lichens is exceptionally high since they represent a massive and easily accessible food, the abundance of which does not undergo seasonal fluctuations. Adaptation to feeding on lichens enables reindeer to survive under conditions of extremely prolonged, severe, and snowy winters whereas other ungulates would die.[336]

In the Far North domesticated reindeer consume about 50 species of lichens (fruticose, tubular, and foliose), of which four species of *Cladonia* are preferred: *Cladonia rangiferina, C. silvatica, C. mitis,* and *C. alpestris* (Aleksandrova, 1940). In the Altai the diet of wild reindeer includes over 20 species of lichens, of which roughly one-half are primary (in addition to the four species already mentioned, *C. amaurocraea, C. uncialis,* species of *Cetraria* and *Usnea,* and *Bryopogon chalybeiforme,* i.e., arboreal lichens). In Lapland preserve the intake of no less than 13 species of lichens has been established, of which *C. alpestris* is most often consumed in the first half of winter, and mostly *Cetraria nivalis* and *Alectoria ochroleuca* in

---

[335] Lichen remains in the rumen of domesticated reindeer (139 animals) of three different regions of the Far North in summer did not exceed an average of one-tenth to one-fourth by weight of the entire food mass, which consisted mainly of different types of green foliage (Aleksandrova, 1940).

[336] In their adaptation to living under conditions of severe Arctic winters reindeer are inferior only to musk ox. According to Palmer's data (1944) the latter are less fastidious in food selection and consume all accessible lichens more fully than caribou. In experiments on feeding with lichens alone (Fairbanks, Alaska), reindeer and caribou utilized 37% of the available food and musk ox 52%.

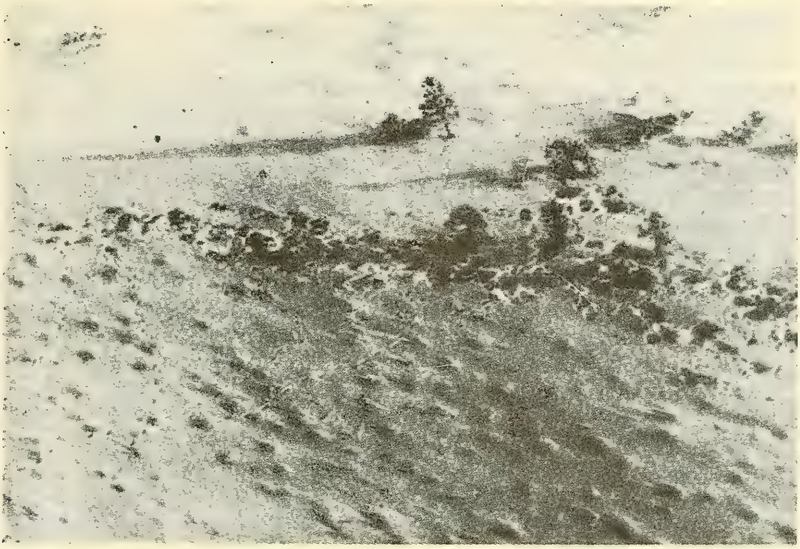


Fig. 107. Place of pasturing of wild reindeer at the source of the Malaya Icha River (Tara River basin, Vasyugan). January, 1957. Photograph by K.T. Yurlov.

the latter half when it is snowier and most wild reindeer live in montane tundra. In the plains and montane taiga regions with a deep snow cover in the second half of winter, arboreal lichens acquire extreme importance (Pechora basin, western Siberia, and elsewhere). This same food is consumed in large quantities when an ice crust forms (Kola Peninsula, Yenisey basin, and elsewhere).

Observations of domesticated reindeer in the Berezov region (Pripolar Ural) and Murmansk district revealed that on a winter day they can consume 5 to 6 kg of terrestrial lichens per animal (weight computed on air-dried basis; Igoshina and Florovskaya, 1939; and others). Lichens are well utilized only in a wet state. They are less
334 liked in summer than in winter, not only because at that time of year green fodder is available, but also because on some days lichens have dried to such an extent that they begin to crumble on the slightest contact.

Reindeer consume herbaceous vegetation year-round. In winter plant parts which remain green under the snow (this phenomenon is widely prevalent in the north) are of utmost importance but dried material is also consumed. In summer, along with herbaceous vegetation, leaves of some shrubs and trees are also well consumed. These, like green plants, are considerably richer than lichens in proteins and mineral matter. An abundant intake of green plant parts in the latter half of spring and summer makes it possible for reindeer to restore the metabolism disturbed during winter.

From among herbaceous vegetation reindeer consume grasses, sedges, horsetails, and forbs, the importance of the latter, well consumed in summer, is paramount. In northern regions of the USSR domesticated reindeer consume 268 species of green plants, including 6 species of horsetails, 37 of grasses, 35 of sedges, 32 of shrubs (willow and birch), and 154 of forbs; of the latter, 20 to 25 species are of paramount importance (Aleksandrova, 1940). The intake of 50 species of herbaceous plants (forbs, grasses, and sedges) has been recorded in the Altai, of which about one-third are primary dietary items; 4 species of small shrubs and 13 species of shrubs and trees are consumed additionally (but only willow well; Shaposhnikov, 1955).

In summer the green plant content (herbaceous vegetation and leaves of shrubs) in the rumen of domesticated reindeer (139 animals) from three different regions of the Far North averaged 72.0 to 78.5% of the total food mass (Aleksandrova, 1940). In the Malozemel'sk tundra no less than 30 to 40% of the total food consumed is accounted for by willow and birch leaves (*Betula nana* and *B. tortuosa*) (Sdobnikov, 1939; and others).

Judging from observations of wild reindeer in Altai and Lapland preserves, fescue (*Festuca*), *Deschampsia,* meadow grass, and orchard grass are well consumed. These species and *Arctophila fulva* (northeastern Siberia; Tikhomirov, 1937), are also consumed well by domesticated reindeer. From among forbs, wild reindeer take well to willow herb [fireweed], knotweed (*Polygonum*), buttercup, buckbean, sorrel (*Rumex*), crowfoot, *Saussureia,* and many others (Averin, 1948; Semenov-Tyan-Shanskii, 1948; Shaposhnikov, 1955; and others). Cotton grass (*Eriophorum*) and sedges are consumed in maximum quantities in spring, while grasses are consumed at the end of spring to early summer; forbs are consumed well in summer. In Arctic tundra grasses and sedges constitute significant dietary items throughout the year. On wilting, forbs lose much of their importance as food. Grasses, sedges, and cotton grass increase in edibility later. The blades of these grasses, and sometimes even the lower parts of stalks, remain green in the north not only in autumn but also in winter (Aleksandrova, 1940).

Dried plant material and the green portions of plants are consumed throughout winter; their importance is paramount in some mainland tundras and Arctic islands[337] where good lichen is inaccessible because of dense snow. In such cases, as observations on Bogicheva Island have shown, wild reindeer must perforce be satisfied mainly with sedges and grasses emerging from under the snow (Koshkin, 1937).

---

[337] Judging from observations of domesticated reindeer, the proportion of dried and green plant food in the winter diet on Novaya Zemlya averaged 41% of the entire food mass in the rumen (lichens alone 20% and the rest mosses; Aleksandrova, 1937) and in the Malozemel'sk tundra 49% (lichens 51%; Sdobnikov, 1935).

Reindeer eat well the leaves of some berry shrubs, and green stalks of bilberry; they also take avidly to cloudberry, blueberry, bearberry, and crowberry (in spring as well). In Kamchatka, mountain-ash fruits are also eaten well (Averin, 1948). Leaves of shrubs and trees are well consumed not only when green, but also in
335 autumn when they fall; this is particularly true of dry leaves of *Chosenia macrolepis* shrubs, which have no equal in richness of mineral matter and are eaten well by domesticated reindeer in Yakutia (Egorov and Kubaev, 1958).

Reindeer also eat buds of shrubs and trees (of willow in spring; Naumov, 1934) and young shoots not older than a year. Lignified shoots and needles of conifers are usually eschewed. Bark is mostly ignored although in Konda-Sosva preserve the remains of pine bark have been found in the stomachs of wild reindeer several times (V.V. Raevskii). By and large twigs are of secondary importance to reindeer even in taiga regions.

The remains of the mosses *Dicranum, Polytrichum, Mnium, Hylocomium, Hypnum,* and others have been found several times in the rumen contents of wild and domesticated reindeer. In Altai preserve the remains of green mosses comprised 6.0 to 14.7% of the food mass in the rumen of two wild reindeer caught in summer (F.D. Shaposhnikov, 1955). In Novaya Zemlya mosses in winter have averaged 41% (in some cases up to 61%) of the total food mass in the rumen of domesticated reindeer. The remains of liverwort (*Ptilidium ciliare*) have been observed in particularly large quantities in the rumen even though it is relatively sparse in the vegetative cover (Aleksandrova, 1937). The importance of mosses as food is not clear but there can be no doubt that they alone, even in such large quantities, often do not meet reindeer food requirements. It is interesting to note that green mosses represent one of the main food items for other inhabitants of the Far North, i.e., lemmings. Ferns and club moss (*Lycopodium*) are rarely eaten by reindeer.

The avid intake by wild reindeer of capped mushrooms, and "fungi" in general has been noted repeatedly (Cherkasov, 1884; Sokol'nikov, 1927; Naumov, 1934; Novikov, 1937; Plechev, 1939; Belyk, 1948; Shaposhnikov, 1955; and others). Domesticated reindeer are relatively less attracted to mushrooms in summer, but search them out in autumn and dig them up from under the snow "until late in winter" (Sdobnikov, 1939). Domesticated reindeer of the Pripolar Urals wander extensively in years of abundant availability of mushrooms, seeking this food item (Igoshina and Florovskaya, 1939). The species composition of mushrooms consumed by reindeer has yet to be analyzed.

A deficiency in proteins and mineral matter in their diet and the consequent metabolic disturbance[338] often compel reindeer to turn to animal and other food sources not consumed by most other ungulates. Feeding on lemmings by domesticated reindeer has been observed several times; instances are known when reindeer destroyed clutches of eggs and killed nestlings and ate dry meat and fish (Palmer, 1927; Sdobnikov, 1935). The stomach of a wild reindeer caught in summer in the Altai contained the remains of voles (F.D. Shaposhnikov, 1955). Wild and domesticated reindeer eat the epidermis of antlers and often gnaw at shed antlers and old bones. Innumerable reindeer and elk antlers, gnawed at the ends by reindeer, have been found in Lapland preserve (Semenov-Tyan-Shanskii, 1948). Female domesticated reindeer gnaw the tips of antlers still on the head of their calves (Alaska; Murie, 1935).

Reindeer are extremely fond of salts and human urine, especially of snow wetted with urine, since protein and mineral deficiency are more pronounced in reindeer in winter. While licking urea reindeer can assimilate simple nitrogen compounds and, perhaps, even inorganic nitrogen and are helped in this process by the microflora of the rumen (Druri, 1949). Reindeer avidly lap mineralized water, lick ice on river and marshy ice crusts, and visit watery salt licks in some regions in summer (Cherkasov, 1884; Naumov, 1934; Shaposhnikov, 1955; and others). In Lapland preserve in the period of estrus wild reindeer were found to consume soil (Semenov-Tyan-Shanskii, 1948). On sea coasts reindeer lick salts, lap sea water, and consume *Laminaria*[339] and other algae (Sdobnikov, 1935; Flerov, 1935; and others).

336 In winter the moisture intake of reindeer is limited to the minimum metabolic needs of the organism since licking snow leads to a significant loss of body heat.

Home range. The territorial behavior of wild reindeer has not been studied well. Skalon et al. (1941) suggest that within Taimyr there are several fairly isolated populations of wild reindeer, each of which is characterized by a definite place of summer residence, migratory routes, and wintering sites. Similar reports are available for other regions of Siberia, especially the reindeer population inhabiting the New Siberian Islands (Pinegin, 1932). These accounts are obviously correct but supported by very little factual data.

---

[338] A mineral deficiency in reindeer is caused not only by an abundant intake of lichens, but also by the substitution of snow for water for several months; snow is poor in salts (Formozov, 1946).

[339] In Spitsbergen these algae represent not only a delicacy, but also an important early autumn feed for reindeer (Flerov, 1935).

In summer wild reindeer live in small groups or singly while adult females live with fawns. At that time of year reindeer in Lapland preserve do not wander much but live in a definite section of the habitat, which possibly does not change over several years. Some observations have been made on wild reindeer and domesticated animals which had turned feral living together. In one instance a distinguishable single wild male was sighted in mountain tundra at the end of July and again in mid-August at a distance of 3 km from the point of first observation (Semenov-Tyan-Shanskii, 1948). Small groups of wild reindeer largely confined to small areas have been noted in summer (Druri, 1949).

In the period of estrus reindeer congregate in definite regions. On the Nyavka tundra (6,000 hectares) of the Lapland preserve several reindeer herds have been identified during the period of estrus, "each herd in its own section"; migrations of herds from one place to another do occur but are not typical; herds with harems are quite isolated and generally less mobile. Often, even at the end of estrus, a herd will remain intact in the same region and not split up (Semenov-Tyan-Shanskii, 1948). In winter, on the contrary, great mobility is characteristic of wild reindeer[340] and observed in taiga and mountain-forest localities, and in more sharply expressed form in tundra zones and the Arctic islands. In Novaya Zemlya, for example, reindeer live in winter sometimes in the southern and at other times in the northern islands, depending on food and other conditions, undertaking migrations extending over a few hundred kilometers.[341]

Reindeer herds wintering close to the Taimyr coast and in adjacent islands where winter migrations between the mainland and the islands and from one island to another are not a rare phenomenon, are characterized by exceptionally great mobility (Koshkin, 1936; Rutilevskii, 1939; and others). In eastern Taimyr reindeer remain for some days within relatively small (2,000 to 3,000 hectares) sections of the tundra in winter but as soon as all available food is consumed, wind direction changes, or the animals are frightened, they leave for another section (Shastin, 1939).

---

[340] Domesticated reindeer, compared to wild animals, are characterized by lesser mobility since they are less fastidious in feeding habits and eat available food more thoroughly; their mobility is nevertheless greater in winter than in summer.

[341] A tagged domesticated reindeer from the southern island of Novaya Zemlya attached itself to a herd of wild reindeer and was caught on Cape Zhelaniya, representing the northern extremity of Novaya Zemlya (Klyuge, 1936).

In taiga forests of the central part of the Yenisey basin reindeer sometimes migrate briefly over a few tens of kilometers and for 100 km or more during winter (Naumov, 1933 and 1934). Similar events are known in other sections of the forest zone, including regions close to the southern boundaries of the reindeer range where they are not found at present (Eversmann, 1850; Middendorff, 1869; Kolosovskii, 1884; and others).

Extensive winter migrations, sometimes over tens of kilometers, are also characteristic of reindeer of Lapland preserve. Observations have shown that there is no definite localization of individual groups at that time; much of the area suitable for wintering is shared by reindeer inhabiting the preserve. A herd of 50 to 60 animals with several leaders was sighted at the end of November at the southern
337 boundary of the preserve and at the end of February at the northern boundary at a distance of 40 km from the first site (Semenov-Tyan-Shanskii, 1948).

Winter migrations of reindeer depend largely on the weather regime. The animals usually move against the wind, which not only facilitates the timely detection of danger, but also reduces loss of body heat since under these conditions the wind does not penetrate between the hair. In spite of the great mobility of reindeer in winter, the territory on which they actually live and feed at that time of year is usually much less than in summer. For example, in Lapland preserve the local reindeer population (about 1,000 animals in 1940 to 1941) occupied in summer a territory of 150,000 to 2,00,000 hectares, while in the latter half of winter they congregated in an area of about 20,000 hectares; even in this small area only about one-half of it represented pasture land and the remainder was visited by reindeer during migrations (Semenov-Tyan-Shanskii, 1948). As a result, the density of reindeer population in winter, compared with that of summer, was 7 to 10 times greater (50 animals per 1,000 hectares versus 5 to 7 in the same area during summer). The capacity of winter pasturing grounds for sustaining wild reindeer in Lapland preserve has been determined as a minimum of 2,000 animals (N.M. Pushkina); thus, the foregoing high population density did not yet represent the maximum.

Reindeer utilize a significantly smaller territory in winter than in summer, but the animals wander extensively, visiting periodically one or the other pasturing grounds which are more suitable at a given time with respect to snow regime and other grazing conditions. In most regions the reindeer population is usually limited not by summer pasturing grounds, but by the availability of wintering sites. For example, in Gusinaya Zemlya (southern island of Novaya Zemlya) a minimum of 2,000 reindeer might graze in summer, which in winter may not exceed 500 to 600 (Zubkov, 1935; Aleksandrova, 1937). Experience of reindeer husbandry has shown that in most pasture lands, without interfering with the restoration of reindeer moss, four to five times fewer reindeer can feed in winter in a given area than in summer (Druri, 1949).

In Soviet literature norms are repeatedly cited for reindeer pasturing areas in Alaska as determined by Palmer (1927 and 1934). This author believes that reindeer in summer need 4 to 6 hectares (sometimes not more than 3.2 hectares), but in winter 12 to 18 hectares, the average for the year being 16 to 24 hectares (the lower value for southern regions and the higher for northern). These norms are not at all applicable to wild reindeer (as stated by Palmer himself in his 1944 work) since wild animals are more mobile and selective in diet than domesticated reindeer and need protective cover to a much greater extent; when wild reindeer live in crowded conditions, they easily fall prey to diseases.

Daily activity and behavior. In summer, under polar day conditions, periods of activity (grazing and migrations), subsequent rest (lying or standing), and rumination alternate several times a day[342] and vary on different days depending on the weather and number of blood-sucking flies at different hours. In the coastal tundra of northern Siberia and in Arctic islands blood-sucking flies are almost absent and do not influence the daily rhythm of reindeer there.

In summer in eastern Taimyr wild reindeer (Shastin, 1939) graze in the early morning hours, from 9:00 to 10:00 a.m., rest from 11:00 to 12:00 noon, and feed later for four to five hours; from 5:00 to 7:00 or 8:00 p.m. the animals again lie down and feed later; the next rest period is usually from 1:00 to 3:00 a.m. to 5:00 to 6:00 a.m. In Lapland preserve reindeer in summer follow no strict daily rhythm (Semenov-Tyan-Shanskii, 1948) but never graze in the warmest hours of the day.

In the Altai mountains in July–August, when the weather is warm, reindeer are confined during the day to shaded slopes in the alpine belt in the mountains, often to snowfields where it is cooler, blood-sucking flies and gadflies absent, and fresh green foliage, is available nearby. During midday hours wild reindeer can be seen

---

[342] Three to eight times, on the average six times, in domesticated reindeer in the Pri-polar Ural (Igoshina and Florovskaya, 1939).

338 lying on the snow, shifting from place to place, or even standing on mountain crests where the wind is strong as measures to protect themselves from blood-sucking flies. In the evening reindeer descend to the upper sections of the forest belt to graze, and in the morning, as soon as the sun dries the dew, ascend again (Dmitriev, 1938; F.D. Shaposhnikov, 1955). Reindeer of other montane regions also rescue themselves from blood-sucking flies on snowfields (Sayans, Khamar-Daban, Kamchatka, and others).

The usual method of escaping from blood-sucking flies (in the morning and during the day from gadflies, horseflies, and midges, and in the evening from mosquitoes) is by shifting from place to place, which accounts for the formation of most reindeer trails where the animals are abundant. Very often reindeer also go to much higher, more windblown places, congregate close to open banks of large rivers and lakes, while in tundra and forest-tundra they enter shrub by places, or in the forest zone, go into open marshy expanses and into open woodlands. In western Taimyr during mass flights of blood-sucking flies the animals from deep inside the tundra go out to the sea coast where the wind is strong (Heptner, 1937). In eastern Taimyr in July reindeer were found lying in water on river banks as a refuge from mosquitoes and midges; the water temperature was 7 or 8°C (Shastin, 1939).

338 Fig. 108. Trail of wild reindeer in pine grove covered with reindeer moss. Lapland preserve. Photograph by O.I. Semenov-Tyan-Shanskii.

Reindeer suffer in summer not only from blood-sucking flies, but also from heat since much of their skin is devoid of sweat glands. After intense muscular activity the mouth hangs open and the tongue protrudes. Contrarily, on the sea coasts of Siberia and in the Arctic islands reindeer are very sensitive in spring and early summer to intense and prolonged cold winds, especially when they are accompanied by snowfall. The animals then look for protection under high banks, hide in ravines, or penetrate deep into the tundra far away from the sea (Heptner, 1937; Koshkin, 1937; Shastin, 1939).

In Lapland preserve during transitional seasons (April and September–October) reindeer are evidently more active at dusk and at night and often lie down during the day (from 9:00 a.m. to 3:00 p.m.) (Semenov-Tyan-Shanskii, 1948). The daily activity of wild reindeer in winter is almost unknown.[343]

339 Reindeer can withstand extreme subfreezing temperature in windfree conditions more readily than a temperature of 8 to 10°C in strong wind. References are available to show how wild and domesticated reindeer, even before the onset of a snowstorm, exhibit restlessness and attempt to find a calmer place in good time by descending from mountains into boreal forests, crossing into forests from large swamps, seeking protection from open tundra under elevations, and so on (Turkin and Satunin, 1902; Kozhanchikov and Kozhanchikov, 1924; Goncharov, 1930; and others). However, during a snowstorm reindeer of Lapland preserve often remain in the same open pasture in the mountain tundra, most often lying with their side to the wind and the head turned leeward; the animals allow themselves to be covered with snow.

Reindeer hooves are very broad, especially those of the forelegs, and can be spread widely; the lateral digits are well developed and the lateral hooves provide additional support while walking. By winter time the contact surface of the hooves has increased since the horny material has increased; the hair brushes between the digits, which cover part of the padded side of the hooves, also enlarge. The weight load on the hoof surface of reindeer is 140 to 180 g per cm^2 (Seton, 1909; Semenov-Tyan-Shanskii, 1948; Dul'keit, 1956), i.e., more than in the case of musk deer and less than that of other Russian ungulates. The hoof surface is slightly concave and the fore end sharp, representing an adaptation to digging snow (Tarasov,

---

[343] The daily activity of domesticated reindeer in different seasons of the year, including winter, has been studied in detail by Igoshina and Florovskaya (1939) using chronometry. Much of their data are of general interest and enable us to understand the biology of wild reindeer also.

1956) and simultaneously preventing slippage on slopes covered with crusted snow. The limb joints are unusually mobile; the animals can raise their legs high or bend them to form an acute angle; this ability facilitates movement of soft snow, among hummocks, and in shrubs. On the whole, the structure of the legs and hooves serves as an excellent adaptation to living under conditions of prolonged and snowy winters.

The usual form of movement is pacing or an even trot, and sometimes galloping. Extremely frightened reindeer gallop (jumping 5 to 6 m downhill) but soon change to a trot. The rate of pacing is 2.5 to 3.0 km an hour and of trotting and galloping 3.5 to 5.0 km an hour (Shastin, 1939). Reindeer crossed a swamp about 45 km wide during winter migrations in the Poronaysk valley (Sakhalin) in 1.0 to 1.5 days (E.P. Volkova).

In spite of being well adapted to living under conditions of snowy winters, the ability of reindeer to negotiate deep snow cannot be rated high. In a soft (0.15 to 0.20) snow cover of over 50 to 60 cm deep some reindeer begin to experience difficulty in walking; when the snow height is 80 to 90 cm, difficulty is experienced even by animals in a herd, although in this case tired animals can use the tracks made by animals in front. In montane forest regions, as soon as the snow height in the forest builds up to roughly half a meter, many reindeer move over to mountain tundras where the snow cover is dense and therefore readily negotiated (Teplov and Teplov, 1947; Averin, 1948; Semenov-Tyan-Shanskii, 1948).

Domesticated reindeer can reach food situated under soft snow 90 to 120 cm deep, but even at a snow depth of 70 to 80 cm the energy expended by the organism in digging up the snow is usually not compensated and the animals lose weight. Wild reindeer, unless compelled to do so, do not dig in snow over 50 cm deep; they prefer to wander extensively and search for more accessible food (Semenov-Tyan-Shanskii, 1948). If the snow cover is dense (0.28 to 0.36), wild animals insofar as possible select places where the snow is no more than 5 to 10 cm deep (in completely snow-free sections food is usually poor in availability and quality) and dig up moss; more rarely they dig in snow 15 to 20 cm deep and even less often 25 to 30 cm (montane tundra of Lapland preserve; Nasimovich, 1955). In Novaya Zemlya, at a snow density of 0.20 pasture is accessible to domesticated reindeer for grazing at a snow depth of over 50 cm; when snow density is 0.30 grazing grounds are accessible only at places where snow depth is less than 50 cm; and when snow density is 0.40 accessibility is limited only to sections where snow depth is not more than 20 cm (Aleksandrova, 1937).

Reindeer can smell moss under snow up to one meter deep; having begun to dig the snow, they usually trace moss by smell. Deep snow is dug up with the hooves, while shallow, loose snow is scattered with the head. The animals catch only the uppermost portions of the moss fronds between their lips and do not uproot
340 the plant. Wild reindeer do not feed in areas full of snow-filled holes formed as a result of previous grazing, since the snow there is deeper.[344] All this promotes the regeneration of moss (Semenov-Tyan-Shanskii, 1948).

Both wild and domesticated reindeer often make use of favorable features of the topography and vegetation, which facilitates access to food under snow.[345] They dig up lichens in uplands, hummocky swamps, and so on. Domesticated reindeer on setting out to dig in a sparse birch-larch forest begin by scattering the snow first under large trees, close to the base where the snow is less, and later dig in a direction where there is more food (forest-tundra of the Nadym River basin; Avramchik, 1939). In eastern Taimyr wild reindeer in winter often go to the coastal cliffs by the sea and feed there on lichens readily accessible on rocks (Shastin, 1939).

Reindeer swim well and can successfully negotiate not only large rivers swollen with water (Yenisey, Taimyr, Anadyr, and others), but also marine straits a few kilometers wide. Instances are known of reindeer attempting to swim from ice floes across the 120 km wide Dmitrii Laptev Strait, but the animals died in the process (Pinegin, 1932).

Of the senses, olfaction is best developed in reindeer. In the Altai the animals keep away from man, moving downwind, at distances of up to 4 km (Shaposhnikov, 1955). When reindeer are frightened by something, they attempt to move in a leeward direction [downwind] in order to assess the situation with their olfactory faculty. The auditory organs are well developed and vision moderate. In an open place, with a background of snow, reindeer can spot other reindeer or man from roughly a kilometer away, but begin to react only when movement occurs. As soon as even a single animal in a herd is disturbed, the others follow its example (Semenov-Tyan-Shanskii, 1948). Invariably the same adult males or females act as leaders of the herd (Shastin, 1939; and others).

The herd strength of reindeer depends largely on their population. The largest herds, comprising several thousand animals, have been sighted in northern Siberia during autumn migrations. In autumn a herd of up to 1,500 to 2,000 animals has been recorded in Kronots preserve and a herd of up to 830 animals counted in winter in Lapland preserve. Large herds are transitory and easily split into smaller groups.

---

[344] Of necessity domesticated reindeer often behave differently.

[345] Similar observations have been made about reindeer movement on soft snow.

Apart from seasonal migrations, which do not occur everywhere, herd strength is usually maximum in winter, especially in March–April when the area of places suitable for grazing is minimum. Winter herds are formed by the fusion of much smaller groups, some of which have survived from the period of estrus. These herds are of mixed composition but adult males stand somewhat aloof from the group (Lapland preserve) or move separately from females.

Among reindeer wandering within a given locality, large herds ultimately break up from the end of April to the first half of May, after which small groups form of fawned females, independently moving fawns of the previous year (sometimes together with barren females and single adult males), and small groups or solitary adult males. Tundra reindeer depart for the north in relatively large herds from wintering sites in the forest zone and forest-tundra. Adult males and females with juveniles (up to two to three years) move in separate groups and at different times (see section "Seasonal Migrations and Transgressions"). Reindeer arrive in the Arctic tundra in small groups (Rutilevskii, 1939). In summer one can see solitary animals (females with fawns), groups consisting of adult males (usually not more than a dozen), or groups of females with fawns (in rare cases up to fifty); yearlings often move with females also.

Seasonal migrations and transgressions.[346] Over a considerable stretch of the range extensive seasonal migrations are characteristic
342 of reindeer. In some regions where such migrations were a regular phenomenon some decades ago, however, as a result of a sharp reduction in the reindeer population they have now ceased (eastern part of Kola Peninsula, southern regions of Yamal, region of New Siberian Islands, Kolyma and Anadyr basins, Chukchi Peninsula, and so on) (Fig. 109). A series of factors are involved in the evolution of these migrations: snow cover regime (depth, density, structure, and duration), severity of winter, summer temperature regime, density of blood-sucking flies, nature and distribution of pastures, intensity of their utilization by reindeer farmers, population of wild reindeer, and so on.

While inhabiting various natural zones and terrains, reindeer usually select areas for wintering where food is most accessible at that time (mainly terrestrial or arboreal lichens, and in the Arctic, grasses and sedges as well). In forests and forest swamps regions with a snow cover of not more than 60 to 80 cm, in mountain and plain tundras areas with no more than 20 to 30 cm, and in Arctic islands tundra with no more than 10 to 15 cm, represent the most favorable areas for wintering. In selecting summer pastures importance is mainly given to the availability of places in which refuge from blood-sucking flies and the heat of the day is insured.

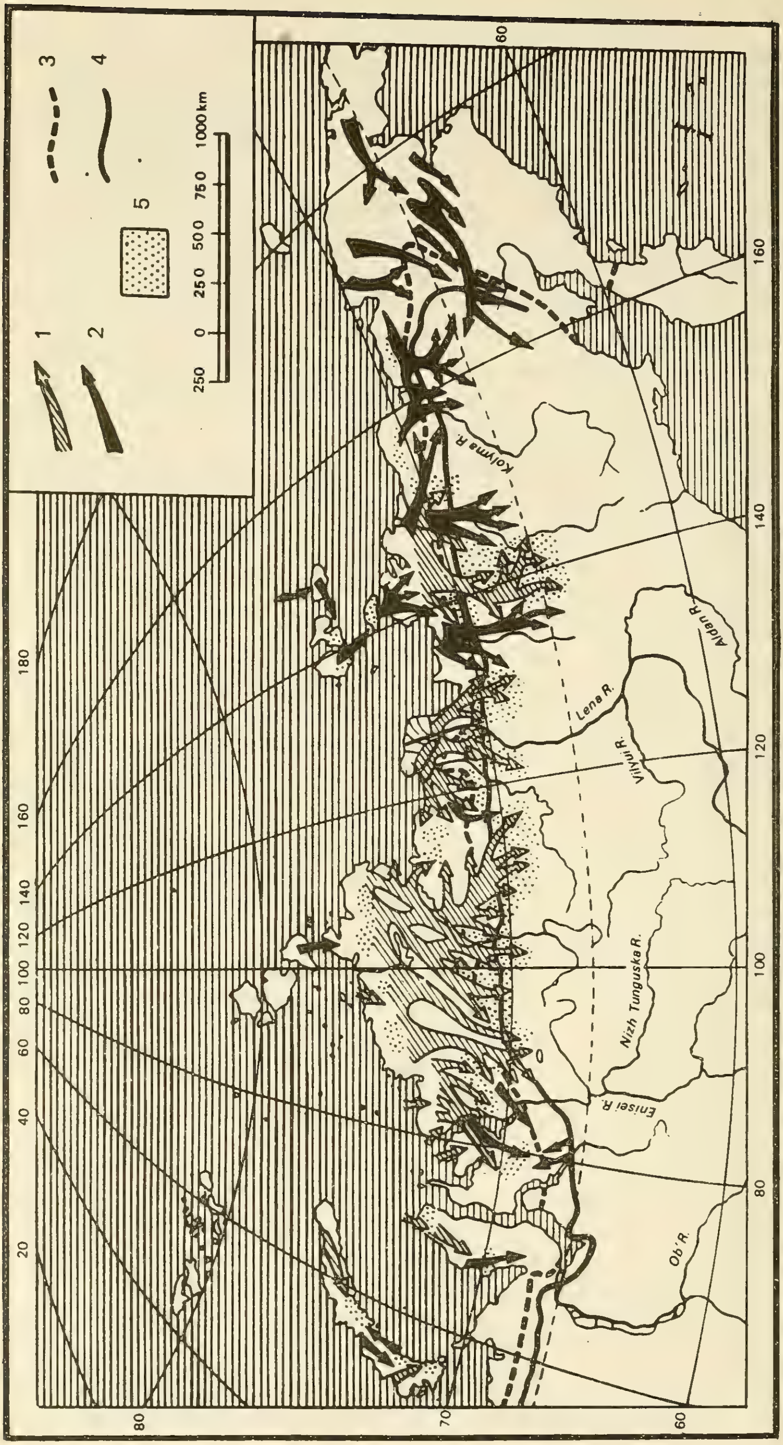
---

[346] Detailed references to sources used in this section will be found in the work of Nasimovich (1955).

Seasonal migrations of reindeer in arctic and subarctic regions are characterized by a maximum range: in polar islands up to 300 to 500 km, and in northern extremities of the mainland at the meeting place of two different natural zones—tundra and taiga—up to 200 to 750 km (Fig. 109). The main reason for the mass migrations of reindeer in winter from the tundra to the forest zone is the difference between the considerable reserves in the former zone of summer food and extremely limited winter food sources; the accessibility of the latter is considerably hindered by dense snow cover. Based on the experience of reindeer husbandry in the Soviet Union, Druri (1949) indicates that four to five times fewer reindeer can graze in a given area of the tundra in winter than in summer. Wandering in winter from the lowland tundras into the forest zone, reindeer disperse in the latter over a large area and winter both in the forest, and in mountain tundra. Wintering of tundra reindeer in the forest zone on mountain tundra (balds) and mountains with sparse forests is particularly characteristic of the interfluve region of the Yenisey and Khatanga. It was also characteristic in the past of the highly snowy Anadyr basin (wild reindeer are currently almost extinct in the Anadyr basin).

On polar islands wintering of considerable numbers of reindeer is possible only under conditions of montane topography and when fairly large areas of pasture grounds are available (Novaya Zemlya), which facilitate the selection of sites with the most favorable snow cover regime for winter grazing.

In mountain forest regions reindeer winter in the forest and mountain tundra (alpine) belts. Wintering in high mountains (throughout the winter or in the latter half of it) is particularly characteristic of abundantly snowy regions of the country; western part of Kola Peninsula, western Sayan, Sakhalin, Kamchatka, Anadyr, and Kolyma ranges. Some of these mountain ranges extend across prevailing winter air currents, as a result of which much of the snow is precipitated on only one slope (windward) and a "snow shadow", where the snow is significantly less, is formed on the other side (Urals, Kolyma ranges). In such regions extensive reindeer


1
2
3
4
5
250 0 250 500 750 1000 km
20
40
60
80
100
120
140
160
180
80
100
120
140
160
60
80
70
60
Ob' R.
Enisei R.
Nizh Tunguska R.
Vilyui R.
Lena R.
Aldan R.
Kolyma R.

migrations have been recorded in the past. For example, in the Urals reindeer congregated in winter in the less snowy pine groves and swamps of the Trans-Urals in summer some moved into the Pri-Urals. These migrations occur even now to some extent.

The distance of seasonal migrations of reindeer in montane forest regions varies from several tens to 100 to 180 km (Urals, Patom uplands, Kamchatka), while the range of vertical shifts usually does not exceed 1,000 m.

343 In the lowland taiga the magnitude of seasonal migrations of reindeer is usually less but in the southern parts of the range ([upper] Volga region, Vasyugan, and others), where land with abundant lichens is inadequate, it reaches 100 km or even more.

In neighboring regions, or even within a given region, different herds of reindeer often exhibit dissimilar modes of life. Some reindeer groups, albeit very few, live year-round in the mainland tundras of the north ("stagnant" reindeer in local terminology); others wander there in winter from the polar islands ("sea" reindeer); others, more numerous, spend the summer in tundras and migrate in winter far southward ("floating" reindeer[347]), and so on. Evidence is available that these reindeer groups differ morphologically.

Wherever the reindeer population has shrunk, the extent of migrations has also steadily fallen. Small numbers of reindeer can find adequate and convenient places for wintering even in the more northern regions and hence the primary stimulus for migration has disappeared.

The general direction of migrations as well as the routes, especially the points of crossing rivers, remain fairly constant, sometimes over a number of years. In the forest-tundra and taiga migratory reindeer are often confined to forest-free uplands and rocky ranges covered with montane tundra. Crossing the tundra reindeer move along the foothills of uplands and along river valleys (Taimyr; Popov, 1939). In spring, turning northward, reindeer avoid excessively snowy regions and move at night during thaws when an icy crust has formed. In the forest they attempt to confine

[347] Swimming through rivers during migrations.

---

341 Fig. 109. Main directions of autumn migrations to wintering sites of wild reindeer of arctic and subarctic regions of the Soviet Union (scale in km).

1—main directions of recent reindeer migrations to wintering sites; 2—main reindeer "currents" to wintering sites which disappeared after population reduction; 3—northern boundary of forest-tundra; 4—northern boundary of taiga; 5—wintering sites (from Nasimovich, 1955).

themselves to smooth tracks formed in the snow by reindeer herds preceding them. At favorable places the herd scatters widely and moves leisurely, grazing on the way.

The change of the landscape resulting from forest fires and road building, damage to reindeer moss, intense hunting on the routes of migrations, and so on, quite often lead to a change in the migratory routes of reindeer. The wind regime also exerts a notable influence (Druri, 1949).

The periods of reindeer migrations and their overall duration depend on climatic and weather factors in individual regions. In autumn reindeer migrations to wintering sites in different parts of the country occur from August (more often from September) to early November, being earliest in regions with a severe climate (extreme north of Siberia)[348] or abundant snowiness; the overall duration of autumn migrations in individual regions is not more than 1.5 months. In most regions reindeer begin the southward migration long before living conditions there become distinctly unfavorable for them. General changes of landscape and of weather from summer to winter as well as individual factors serve as direct stimuli for migrations. Such factors are: the appearance of autumn coloration of vegetation, withering of grass, winter features (cold waves, snowfalls), and in the northern outskirts of the mainland, variation in pressure gradient and the resultant change in prevailing wind direction (wild reindeer often perform migrations moving into the wind). An early, mild winter usually leads to an earlier, easy migration of reindeer, while a late [arriving] winter prolongs the period of migration.

Turning southward from the tundra, reindeer move initially in small groups and later in large mixed herds[349] in which males and females move together. Subsequently the herd size decreases since the general course of reindeer in the forest zone begins to split into
344 individual herds (Druri, 1949). Reindeer setting off first to wintering sites cross rivers by swimming, while those setting out later walk across on ice. In some years the length of the route and hence the place of wintering sites of tundra reindeer vary considerably.

The subject of where and how tundra reindeer of the Soviet North, migrating southward, enter the period of estrus has not been studied. One can only assume that such animals come into estrus in

---

[348] Reindeer move over to the mainland from polar islands usually only in October–November, after the straits have frozen.

[349] Instances have been noted in the nineteenth century, and even in the first quarter of the twentieth century, of migrating reindeer in northern Siberia moving in herds of several thousands.

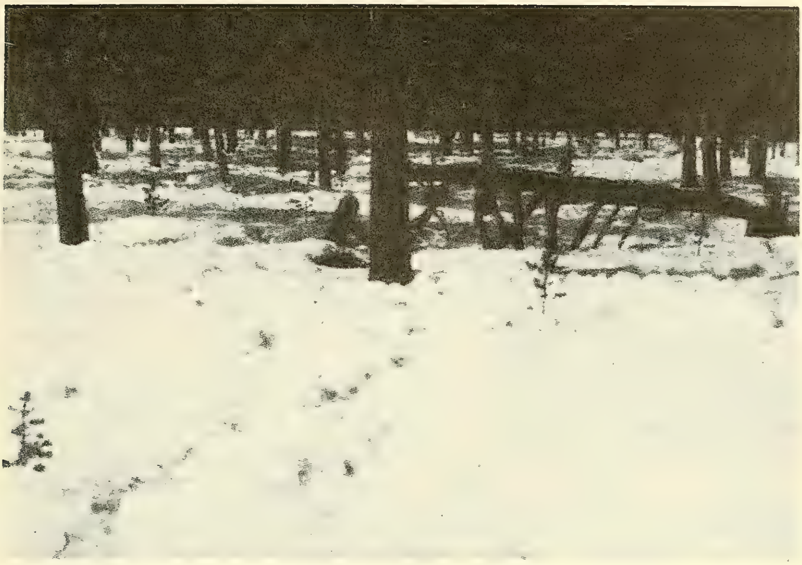


Fig. 110. Tracks of a disturbed herd of wild reindeer in pine grove with reindeer moss ground cover. Lapland preserve. April, 1951. Photograph of O.I. Semenov-Tyan-Shanskii.

the southern tundra and forest-tundra, remain there for two to three weeks, and move away to wintering sites only at the end of estrus. Animals pass the period of rut on Arctic islands since, at that time of year, the straits are still open. Canadian tundra caribou reach the forest-tundra in September but later move northward where they come into estrus at some fixed sites, moving to wintering areas at the end of October–November or even in December (Banfield, 1957).

The spring migration of reindeer from the forest zone to the summer habitation in the tundra begins very gradually even before the commencement of intense snow melt, most often in April. Reindeer move far more slowly than in autumn[350]; in northern Yakutia (Zarovnyaev, 1933) they move at the rate of 3.5 to 4.5 km an hour and not more than 20 km a day. In feeding places the animals may linger for a few days.

In the lower reaches of large Siberian rivers, at the boundary of the forest and tundra, the first migrating reindeer herds are seen in the latter half of May (more rarely even in April) and the last in June. Reindeer wintering in the tundra migrate toward the northern coasts and onto the islands at the end of March–April, usually long before the arrival of forest reindeer. In spring reindeer negotiate rivers on ice or by swimming. Adult males and females at that time of year move in separate herds; the first to commence migration are females with fawns and juveniles up to two years of age.[351] Adult males follow them sometimes after a lapse of two weeks and by other routes. The first reindeer reach the tundra when much of it is still under snow.

---

[350] Caribou migrating in Canada cover up to 160 km on a single autumn night (Seton, 1909).

345 Reindeer wintering in mountain tundras descend into forests in the case of formation of an ice crust which hinders access to food lying under the snow; usually, however, they go into the forest only at the end of April–May, at the peak of snow melt. Reindeer again climb to mountain tundra in summer, after the mass invasion of blood-sucking flies [in the forest].

Wild reindeer are capable of negotiating long distances extending to a few hundred kilometers through regions which are altogether devoid of food. Instances are known when Novaya Zemlya reindeer moved in severe winters on ice into Vaigach and some possibly even into Yamal (Zubkov, 1935; Druri, 1949). Some stray reindeer wandered into Franz Josef Land (established from the finds of antlers and bones) and penetrated from Novaya Zemlya into Spitsbergen (Banfield, 1954). In some years when the ice regime in Vil'kits Strait was favorable, reindeer crossed from Taimyr into Severnaya Zemlya (Bol'shevik Island). Reindeer finds are known from the New Siberian Islands to Bennet Island (Rutilevskii, 1939; Skalon, 1940; and others).

Sightings of reindeer, sometimes sudden and in numbers, have been recorded in regions where they were extinct or had disappeared because of various factors (forest fires and destruction of reindeer moss). This phenomenon was quite significant in the latter half of the nineteenth century in the central regions of the European part of the USSR, when a large number of reindeer arrived from the northern or eastern regions and were seen at several places (Turkin and Satunin, 1902). Commencing from the mid-1920's, mass migrations of reindeer have been recorded for several years in the Nizhnyaya and Podkamennaya Tunguska basins. Reindeer moved from east to west, i.e., from regions where their population was relatively high to places where they were few (Naumov, 1933). The reasons for these migrations have not been studied.

---

[351] Domesticated reindeer which have fawned compulsively move toward places of fawning in spring, i.e., the more northern tundras, and it is difficult to herd them at that time of the year (Zhitkov, 1913; Sdobnikov, 1935).

Reproduction. Within the Soviet Union wild reindeer come into estrus from September to November inclusively. The total duration of the period in which a considerable number of females come into heat does not exceed 2.5 to 3.0 weeks; more often this period lasts for slightly more than two weeks. In different regions of the country the period of estrus varies significantly but information on this subject is extremely contradictory, which is explainable by the difficulty and inadequacy of accurate observations on wild reindeer.

The earliest period of mass estrus of wild reindeer, i.e., from September 10 to 15 to the end of that month or early October, has been recorded for Altai preserve (F.D. Shaposhnikov, 1955), Stanovoi range (Gassovskii, 1927), and Konda-Sosva preserve (V.V. Raevskii). Based on the period of mass fawning recorded for the Altai (from mid-May) and Konda (from May 20 to 31), and taking the duration of pregnancy of reindeer as 223 days, it becomes quite clear that the mass mating of reindeer in the Altai occurs from early October and in Konda-Sosva preserve from around the 11th of that month. From this it is likewise evident that estrus commences in reindeer in these parts of the range later than noted by the above authors.[352] The formation of mixed herds and their congregation at some definite sites is taken as the commencement of estrus; evidently neither bellowing nor mating has yet occurred at this time of year there.

Mass estrus of reindeer commences at the end of September to early October and extends until the end of October in the Sayans (Solov'ev, 1921; and others), in the central part of the Yenisey basin' (Naumov, 1934), and in the central Urals (Galin, 1881). Estrus in wild reindeer in Lapland preserve commences en masse from the end of September and ceases in mid-October (Semenov-Tyan-Shanskii, 1948), i.e., its duration is only slightly over two weeks. Very late periods of estrus, from the second decade [10 days period] of October, have been noted in Kronots preserve in Kamchatka (Averin, 1948), where the peak evidently occurs in mid-November; mating has been
346 observed even at the end of that month. Mass estrus in wild reindeer in Arctic Canada occurs from the end of October to early November (Banfield, 1957).

Based on periods of mass fawning of wild reindeer in the Anadyr basin, Taimyr, and some adjoining islands (Sokol'nikov, 1927; Heptner, 1937; Koshkir, 1937; Rutilevskii, 1939; and others), most female reindeer presumably come into heat in these regions in the latter half of October and early November. This is also true of the northern parts of Taimyr (Sdobnikov, 1958). Estrus in wild reindeer in Novaya Zemlya (Sdobnikov, 1935) and Belyi Island (Tyulin, 1938) also occurs later. In northern Yamal estrus in wild reindeer takes place in October (Dubrovskii, 1940).

---

[352] Error is also possible in observations of the commencement of mass fawning, but less probable.

Thus a somewhat general pattern in the period of mass estrus in wild reindeer is discernible—a significant delay in regions of particularly high snowiness (Kamchatka) and in the Arctic. This may be associated with unfavorable conditions for fawning in early spring (April and much of May). Consequently, the period of fawning is shifted by natural selection to the end of May and June. It is known, for example, that mass fawning of wild reindeer in Novaya Zemlya generally occurs in June, but in domesticated reindeer imported in 1928 and 1929 from Kolyguev Island it took place earlier (from the end of April). Consequently, a large number of domesticated fawns (48% in 1930 and 40% in 1932) died due to cold, snowstorms, inadequate availability of milk from mothers, and so on (Sokolov, 1933; Zubkov, 1935; Sdobnikov, 1935).

Yet some factual data contradict the above phenomenon of delayed estrus in wild reindeer in high altitudes (Shastin, 1939; Druri, 1949). Druri writes about Taimyr: "It is shown that estrus has occurred at much earlier periods in high latitudes and in regions with very severe climatic conditions, where the autumn–spring period sets in early . . . a case is known where hunters caught two females on September 7 in which embryos were found" (p. 29). Such cases should probably be regarded as extreme deviations in the periods of estrus in some animals. Females which mate so early should fawn in mid-April[353] and obviously the chances of survival of their offspring are very poor since winter still continues at that time beyond the arctic circle. Periods of estrus in wild reindeer may vary in different years and quite possibly some disparity in recorded periods of estrus and fawning (rather considerable) should be attributed to nonsequential (sporadic) observations of these phenomena.

The period of mass estrus in wild (September 27 to October 14) and domesticated (September 29 to October 12)[354] reindeer on the

---

[353] As a matter of fact, in the Far North juveniles have been noticed among wild reindeer earlier than early May (eastern Taimyr; Shastin, 1939), the usual period for births being the end of May to the first half of June (Sokol'nikov, 1927; Sdobnikov, 1935; Heptner, 1937; Koshkin, 1937; Rutilevskii, 1939; and others). This period for northern Taimyr is the latter half of June (Sdobnikov, 1958). On Belyi Island fawning commenced in 1935 from June 20 and in 1936 on June 8 (but pregnant females were sighted even on June 16; Tyulin, 1938).

[354] Calculated on the basis of data of mass fawning of domesticated reindeer in the

Kola Peninsula almost coincides. The situation is altogether different in northeastern Siberia where, judging from the periods of fawning of domesticated reindeer in the former Chukotka and Koryak okrugs [archaic administrative district] (Vinogradov, 1936), mass estrus in domesticated reindeer occurs from September 7 to 24.[355] In 1934 matings in Chukotka domesticated reindeer took place from August and through the end of October,[356] the maximum number of females having mated between September 11 and 25 (Shmit, 1936). Among wild reindeer of the Anadyr basin, however, judging from data on the period of the appearance of fawns, i.e., early June (D'yachkov, 1893; Sokol'nikov, 1927), the animals must come into estrus only from around October 20, i.e., a month or so
347 later than domesticated reindeer from regions which are geographically adjacent. Several researchers have noted that estrus usually commences later (sometimes by two to three weeks) in wild reindeer than in domesticated animals (Zhitkov, 1913; Naumov, 1934; Palmer, 1934; and others). Evidently this phenomenon does exist in some cases, northeastern Siberia for example, and should not be regarded as undue prolongation of estrus in domesticated reindeer (so assumed by Semenov-Tyan-Shanskii, 1948; Druri, 1949).

The formation of mixed herds is one of the surest signs of imminent estrus, which in Lapland, Konda-Sosva, and Altai preserves occurs roughly around the same period, i.e., mid-September or slightly earlier. Reindeer at that time (see "Home Range") congregate at definite places—in mountain forest localities mostly in the uplands, sometimes montane tundra, or woodland at the upper forest boundary (Naumov, 1934; Semenov-Tyan-Shanskii, 1948; F.D. Shaposhnikov, 1955), and very rarely in lowland sections. In the period of estrus the water requirement of reindeer is greater and hence they invariably select a place for autumn congregation which has a waterhole or creek nearby.

Molt in reindeer has generally finished by the time estrus sets in and the ossified antlers are free of velvet.[357] Males are nutritionally

---

Murmansk district (Vinogradov, 1936) and of wild reindeer in Lapland preserve (Semenov-Tyan-Shanskii, 1948). We have taken the duration of pregnancy as 223 days and not 220 as assumed by Vinogradov; understandably Vinogradov's computations of the period of mass estrus in reindeer differ somewhat from ours.

[355] The duration of pregnancy in this case had to be 227 days according to Shmit (1936).

[356] A significant prolongation of periods of estrus is quite characteristic of domesticated reindeer.

[357] If molt and formation and peeling of antler velvet in domesticated reindeer are delayed, frequent phenomena among emaciated animals, the commencement of rut is also usually delayed; however, some males invariably come into rut with antlers still partially covered with velvet (Druri, 1949).

near their peak, and their necks quite thickened due to an increase in size of neck muscles (Sokolov, 1935). In the period of rut the adult male exudes an odor easily identified some distance away. At places of reindeer residence during the period of rut small trees and shrubs damaged by their antlers can be seen; some trees are uprooted and characteristic trampled spots occur in clearings and the lichen cover.

Sometimes very large herds form at the commencement of estrus and include some adult males. In Lapland preserve once (September 26, 1937) 7 adult males were counted in a herd of 68 to 72 reindeer; another time (October 1, 1938) adult males numbered 7 to 10 in a herd of 180 to 200 animals. The males bellowed and occasionally fought with each other. Young males were driven away by large stags but more often the latter ignored the former and kept up a continuous bellow. Large herds are not stable and usually split into smaller ones of 15 to 20 reindeer (Semenov-Tyan-Shanskii, 1948).

At places where the overall reindeer population is low the size of harem herds is small. In the Altai preserve they usually consist of one adult male and three to five females (F.D. Shaposhnikov, 1955) and in the Stanovoi mountain range no more than 15 animals (Gassovskii, 1927). In Lapland preserve a herd with a harem usually comprises 8 to 13 females, an adult bull, some fawns (in the period of estrus fawns generally remain with their mothers and are not separated as is the case with red deer), and two or three juveniles or weak males. It may happen that during estrus if the stag in the harem has dissipated his energy early, he is replaced by another male; this is all the more likely since not more than one-half of the adult males in a population (usually about 10%) possess harems. Rival bulls either stay close to the harem herd or wander extensively (Semenov-Tyan-Shanskii, 1948). In domesticated reindeer husbandry an adult male bull (usually not older than six years) should cover 15 to 30 adult females, but instances are known of one bull mating with 40 to 44 females (Alaska).

Fights between adult males over females are frequent but very rarely result in the death of one or the other. Males with broken antler tips are a more frequent sight. Severe combats between males have not been observed in Alaska even once (F.D. Shaposhnikov, 1955). There are no skirmishes among males in the absence of females. In the period of rut males are highly weakened since they
348 eat little and are less vigilant than in other seasons. Sexually excited males emit a sound similar to that of a snore, which is repeated at half-second intervals and can be heard for 200 m. This sound (called "rekhkan'e" by Saams [native people of Kola Peninsula]) bears no resemblance whatsoever to the call of red deer.

Reindeer become sexually mature in their second year but males under three years usually do not mate. Among domesticated reindeer juvenile females usually mate late, i.e., in October–November and even in December, and some only in their third year. Yet instances are known of females pregnant even in their first year and giving birth to fawns (Jacobi, 1931; and others). Even juvenile males become sexually aroused at a much later period. This results in very late fawning, from July to September, noticed from time to time among wild reindeer (Averin, 1948; and others).

Observations on domesticated reindeer in the Nenets okrug and Murmansk district revealed that the duration of pregnancy varies from 192 to 246 days, with an average of 223 days; in Chukotka this duration is 219 to 238, with an average of 227 days. The duration of pregnancy does not depend on age. Females with male embryos have a longer (by 2.7 to 5.4 days) pregnancy period than those with female embryos (Shmit, 1936; Gorbunov, 1939).

Migratory wild reindeer usually fawn in their summer residence. In Lapland preserve fawning takes place most often in dry, relatively warm thawed patches in the forest and probably also in mountain tundra (Semenov-Tyan-Shanskii, 1948). In Konda-Sosva preserve it occurs along small dry ridges and islets among swamps (V.V. Raevskii), and in the Altai in woodlands of the subalpine belt and in shrub tundra (F.D. Shaposhnikov, 1955). The earliest period of mass fawning is from around May 11 (some females fawn even by the end of April), while the last fawning takes place in June.[358] Fawning often occurs in June in Kamchatka and the Arctic and in the latter half of May in Lapland preserve. It quite often coincides with the peak of snow melt in the forest.

During her life span a domesticated female reindeer births 10 to 12, sometimes even more fawns (maximum 30); under optimal living conditions, fawning takes place almost every year (Petri, 1927; Jacobi, 1931; Sokolov, 1935). Only one fawn and extremely rarely two characterize wild reindeer (twins have never been seen in Lapland preserve). In Swedish Lapland instances have been recorded two or three or even four fawns for several consecutive years (Jacobi, 1931). Among domesticated reindeer females have been known to steal the fawns of others and move away with them (Sdobnikov, 1935).

Growth, development, and molt. Newborn reindeer fawns attempt to stand and walk on the same day of their birth and usually succeed in doing so. The tiny hooves are initially soft and yellowish with strongly elongated tips. By the next day the hooves have hardened, the terminal elongation is shed, and the fawns begin to run well (Sokol'nikov, 1927). In their very first week fawns are capable of swimming across broad rivers.

---

[358] According to Sdobnikov (1958) wild reindeer wintering on the northern coasts of Taimyr fawn not before the end of June. When winter is early, such reindeer have almost no chance of seeing their young live.

At birth fawns of domesticated reindeer have three pairs of lower incisors and a pair of lower canines; milk premolars are developed but covered by the tissue of the gums, and erupt only after several days (Sokolov, 1937). Hornlets appear at the end of the second week. The young sport two rows of light-colored spots on the sides; some fawns, however, are totally devoid of such spots. At the age of about one month or slightly earlier molt of the juvenile coat commences and ends three or four weeks later.

Reindeer milk is very fatty and rich in proteins. Lactation continues up to late autumn and sometimes even into winter (Banfield, 1957). The female drives away the young only before fawning again; later, juveniles rejoin their mother and all of them move together for two to three years.

Judging from the weight of embryos in the later stages of growth, newborn Kamchatka wild reindeer weigh about 5 kg
349 (Averin, 1948). An embryo of a large wild reindeer from the Altai weighed 6.3 kg two or three days before birth (Shaposhnikov, 1955). A 14-month-old wild male reindeer caught in early September in Kamchatka weighed 39.2 kg. Males and females in their third year (August to early September) weigh 60 to 75 kg and three- to five-year-old females up to 130 kg. The weight of adult males, judging from the weight of the cleaned carcass (120 kg), can reach 180 kg (Averin, 1948). The largest males among some reindeer caught in Altai preserve weighed 180 kg (August; F.D. Shaposhnikov, 1955), which evidently is far from their maximum weight. Forest reindeer are generally taller than tundra reindeer and their weight greater. Mountain and forest animals differ little in constitution although numerous references to the contrary occur in literature (Skalon, 1951; and others).

Molt in reindeer occurs once a year and continues for a long time. The old underfur starts to shed in March–April, followed by guard hair. In eastern Taimyr reindeer lose hair in April while on the move [migrating], and molt peaks in May (Shastin, 1939) with the new underfur appearing followed soon by guard hair. Molt commences from the head, extending later to the neck, legs, and back, and finally to the sides and belly (Rutilevskii, 1939). Molt proceeds intensely in June and ceases only by the end of July or in early August but, evidently, only by the end of that month in high latitudes in some years (tufts of old hair can remain until September). The fur of reindeer in the first half of summer is uneven with bald spots, and short and dark in July; the hair grows appreciably longer in August and the bald spots disappear. The short coarse hair in July grows through the underfur by August and the reindeer acquires the characteristic autumn coat of gray hair. The winter color of hair, especially of reindeer living in the tundra, is light, which is evidently associated with the gradual fading of hair (Semenov-Tyan-Shanskii, 1948). Molt is delayed in the event of a late and cold spring (Shastin, 1939; and others). Healthy reindeer are the first to molt and emaciated animals last, molting two weeks later (Sokol'nikov, 1927).

Antlers are present in reindeer of both sexes[359] but hornless females are often seen, constituting 25 to 33% of the population in the Sayans and Altai. Sometimes the antlers are underdeveloped and are like stubs without tines (Mashkovtsev, 1940; F.D. Shaposhnikov, 1955). Among fawns in their first year of life, antlers are in the form of mere stubs, straight or bent slightly forward with simple or bifurcate ends. Ossification of antlers and shedding of velvet occur later in juveniles than in adult animals. Velvet starts to slough from the end of September and continues sloughing for most of October. At this time the animals rub their antlers against the trunks of small trees and shrubs. The first antlers are preserved until April–May. In the second year antlers with a crown and foretines are seen. By age four or five years the crown structure becomes complex. Antlers of adult females are considerably smaller than those of males; in size and thickness they resemble the antlers of two-year-old males (Semenov-Tyan-Shanskii, 1948).

In the adult wild male reindeer antlers are shed at the end of rut (in Lapland preserve in November, and in the Altai and Belyi Island in December)[360]; this process takes place at the beginning or middle of winter in two- or three-year-olds which do not experience rut. Adult females shed their antlers in the first few days after fawning (this process occurring in barren domesticated animals in February-April). Among adult males new antlers begin to grow in April; they usually grow longer than their ears by the end of May. Antler

---

[359] According to Tarasov (1956) the presence of antlers in females helps them to protect from other animals the pits they dig in snow in search of food. Adult males at that time of the year have no antlers.

[360] Flerov (1935) and several other researchers have erroneously claimed that adult males lose their antlers throughout winter; in actuality this is true only of castrated domesticated reindeer stags.

350 Fig. 111. Wild male reindeer with velvet antlers killed August 24, 1940. Lapland preserve. Photograph by O.I. Semenov-Tyan-Shanskii.

growth is particularly intense in June. Tender antlers are very sensi-
350 tive to blows and mosquito bites. Antler formation and ossification cease in July or the first half of August (last in high-latitude animals). From August 20, or slightly later, velvet starts to slough in males and this process is completed in the first half of September. In females antler formation is delayed and commences from September 20 to early October (Semenov-Tyan-Shanskii, 1948; and others).

The formation of teeth in reindeer is completed by the third year. At about that age males attain full growth and by age five or six years complete development. The teeth of old reindeer are intensely worn, food intake diminishes, a gradual deterioration of antlers is evident, and the pelage becomes matted. Domesticated female reindeer bear fawns up to the age of 15 years, more rarely up to 20 years. The maximum longevity of domesticated reindeer is 25 to 28 years, more often not more than 15 years (Petri, 1927; Jacobi, 1931; Sokolov, 1935 and 1937; and others); the longevity of most wild reindeer is evidently much less.

Enemies, diseases, parasites, mortality, competitors, and population dynamics. Next to hunting, the maximum loss of wild reindeer population is caused by predators, among which the wolf is primary (Naumov, 1933). The role of diseases, significant in reducing the population of domesticated reindeer (according to Pri-polar records for 1926 to 1927, up to 40% of all deaths; Terletskii, 1932), is secondary under the prevailing low density of the wild reindeer population.

Maximum numbers of wild reindeer are killed by wolves in the forest-tundra, southern tundra, and mountain forest regions; wolves are few or altogether absent at some places in lowland taiga with a deep snow cover. In winter wolves primarily kill males that are emaciated during rut as well as sick individuals and domestic reindeer turned wild. The last mentioned are usually confined to the periphery or rear of a herd being pursued. Of the 13 instances of death of reindeer in Lapland preserve, mainly in the winter months, males comprised 85% and females only 15%, in spite of the fact that the male–female ratio among adult reindeer is 26 : 74; thus the mortality of males is 16 times greater than that of females (Semenov-Tyan-Shanskii, 1948). In the region of the Brooks range (Alaska) sick animals (including one with cysticercosis of the lungs) and caribou with injured legs (Crisler, 1956) predominated among the prey of wolves. It is difficult for wolf to catch healthy and unemaciated adult reindeer. Furthermore such reindeer are also not afraid
351 of wolves and venture within 100 m of the predator (Banfield, 1957). Instances are known (Crisler, 1956) of Alaskan caribou rescuing themselves from wolves without much difficulty. Only once did a wolf chase a caribou for 8 km; otherwise the chase ceases much sooner. If a wolf springs on a reindeer and is unsuccessful in the kill, it will not attempt to chase the quarry further. Wolves pose even greater danger to reindeer fawns in the first few weeks of life. They successfully catch mostly solitary fawns or fawns from a herd when turmoil has been created. It is difficult for wolves to catch fawns with their mothers or those in small herds (Crisler, 1956).

The predatory activity of wolves is selective when they are fewer than wild reindeer (in all of the above examples wolves were few). The damage caused by wolves under conditions in preserves is limited, but under other conditions and a higher number of wolves the loss can be very serious.[361] It should also be remembered that wolves not only kill reindeer, but also scatter them and make normal wintering difficult. These predators (like arctic and other foxes) may also be vectors of rabies, Siberian ulcers, and other diseases.

Reindeer are often persecuted by wolverine, but such persecution is only successful in regions of abundant snow (Pechora basin,[362]

---

[361] In McKinley National Park in Alaska feces of wolves collected in different seasons of the year revealed the remains of adult caribou in 19.8% and of juvenile in 23.2% of the samples (Murie, 1944).

[362] In Pechora-Ilych preserve eight cases have been registered of the death of reindeer caused by wolverine mainly from February to April, i.e., in the period of abundant snow in winter. Two juveniles and six adults were injured; of the latter, two were fawned females (Teplov, 1955).

Sayans, Kamchatka, and Anadyr basin) and when the reindeer population is relatively high. There is no doubt that mainly sick and weak reindeer are killed by wolverine (contrary references in literature should evidently be attributed to author reliance on stories of hunters). In Lapland preserve chasing of wild reindeer by wolverine has been repeatedly assumed from tracks or even directly observed. In every instance of the latter the prey eluded the predator. Wolverine survive in winter mainly on carrion, i.e., reindeer carcasses, and thus play the role of scavengers. With the appearance of wolves in the preserve, wolverines feed on the skeletal remains of reindeer, as do red foxes, golden eagles, ravens, and other scavengers (Nasimovich, 1948). Reindeer skeletons are the main source for survival of wolverines in tundras (Sdobnikov, 1939). Wolverine pose a threat for fawns during the first few weeks of life. In Lapland preserve of four fresh feces examined in summer, three contained remains of the tiny hoofs of reindeer fawns.

Lynx, few in number everywhere, cannot inflict much damage on wild reindeer. In the Altai reindeer remains were not found in the feces of lynx (Dul'keit, 1953). Two instances of death of reindeer caused by lynx were established in Krasnoufim region in the Urals (Pechalin, 1928). Brown bear may attack sick reindeer or newborn fawns, but in our [Soviet] preserves, where bear are many, not one instance of their attacking healthy reindeer is known. In the lower Amur and on the Okhotsk coast the damage caused by bear to reindeer could be quite significant (Abramov, 1954). Without adequate proof, Solov'ev (1921) regarded red wolf as the most dangerous enemy of reindeer in the Sayans. This predator is extremely rare in the Soviet Union.

Arctic and red foxes, and probably also some other quadruped predators pose a danger to newborn reindeer fawns, but evidently instances of attacks by them are rare. In years when arctic fox occur widely in northern Yakutia their predation also extends to domesticated reindeer (Romanov, 1941). Golden eagle, white-tailed sea eagle, and especially raven[363] attack young and sick reindeer, but there is no doubt that these birds are more significant as scavengers. 352 In the winter of 1940 to 1941 four golden eagles survived on the predatory activity of wolves and the availability of reindeer carcasses in Lapland preserve. These birds have never been observed in winter prior to the arrival of wolves (Semenov-Tyan-Shanskii, 1948).

Although they exert some influence on the wild reindeer population, wolves and other scavengers depend mostly on domesticated reindeer. The abundance, rarity, or total absence of wolves in winter in the mainland tundras of the north and in Arctic islands depend on the population there of domesticated reindeer. The northern limit of occurrence of wolves in Arctic islands coincides closely with that of wild reindeer and the range of wolverines with that of domesticated reindeer (Middendorff, 1869). The population dynamics of wolf in the Kola Peninsula and in the basin of the central Yenisey are most closely associated with the abundance of reindeer, including wild ones (Mikhailov, 1868; Pleske, 1887; Naumov, 1934; Nasimovich, 1955). With the extermination of reindeer at the end of the nineteenth century in the Visim area of Sverdlovsk district, wolverines also disappeared there (Nasimovich, 1955). The winter migrations of wolves and wolverines in the tundra (also arctic fox in the tundra) and at places in the forest zone depend on the distribution and migrations of reindeer.[364]

---

[363] Observed mainly with respect to domesticated reindeer.

Reindeer are exposed to various infectious diseases; the maximum losses in reindeer husbandry are associated with Siberian ulcers and necrobacillosis (hoof disease) and to a lesser extent with scabies caused by the itch mite (*Acarus siro* var. *rangiferi*). Large numbers of domesticated reindeer die sometimes during epizootic necrobacillosis and Siberian ulcers (Naumov, 1933; Terletskii, 1932; and others). Other diseases—hoof-and-mouth, pasteurellosis, epidemic inflammation of the lungs, rabies, diarrhea, etc.—are of far lesser importance. Wild reindeer are evidently subject to the same diseases as domesticated reindeer, but are not exposed to as great a risk as the latter because of their lesser numbers and other factors. The nature of epizootic phenomena among wild reindeer has never been studied and information about various diseases is confined to reports of individual cases. References are available about Siberian ulcers, necrobacillosis, and hoof-and-mouth disease among wild reindeer (Jacobi, 1931; N.P. Sokol'nikov, 1927). During epizootic scabies in the Nizhnyaya and Podkamennaya Tunguska from 1924 to 1932, even wild reindeer were affected (N.P. Naumov, 1933). Scabies was also observed among reindeer in 1934 and 1935 in the northern extremity of Siberia (Skalon, 1940). There are reports on the death of a large number of wild reindeer due to an unknown epizootic disease in the 1940's in the Yana-Indigirka tundra (Molodykh, 1931), in the 1860's in the former Nizhegorod province (Turkin and Satunin, 1902), and in 1907 in the former Petrozavodsk district (Blagoveshchenskii, 1912). In McKinley National Park (Alaska) cases of actinomycosis have been reported for caribou (Murie, 1944).

---

[364] Arctic foxes trail reindeer in search of carrion. Romanov (1941) erroneously states that arctic foxes are attracted to the grazing grounds of reindeer because digging for lemmings is facilitated there. Actually reindeer graze in the least snowy sections where lemmings usually do not winter.

The helminth fauna of wild reindeer has never been studied either. Over 20 nematodes and cestodes are known for domesticated reindeer; cysticercosis and echinococcosis (Choquette et al., 1957)* and nematode infection of the brain caused by *Elaphostrongylus rangiferi* (Mitskevich, 1958) are widespread. Protozoans parasitizing domesticated reindeer include various species of *Coccidium* and *Sarcocystis,* some of which are specific to reindeer. *Theileria* (*Gonderia*) *tarandi rangiferi* causes disorders of the spleen, sometimes terminating in reindeer mortality.

Four-fifths of the rumen content of reindeer consists of pasture food and related extraneous matter, the balance consisting of microfauna (Igoshina, 1936), mainly protozoa of the family Ophryoscolecidae (28 forms have been identified, including several which are specific to reindeer) and one species of Holotricha. Many protozoans have also been detected in wild reindeer from Novaya Zemlya (Dogel', 1934). Microfauna of the rumen play no small role in rendering digestible coarse cellulose plant material; as a result of bacte-
353 rial activity, much of the plant mass is subjected to the action of digestive enzymes. Protozoa present in the intestines also assist in the digestion of plant material (Sdobnikov, 1935).

In many regions of the country gadflies are a serious pest in reindeer husbandry, attacking the skin—*Oedemagena tarandi* and nasopharyngeal area—*Cephenomyia nasalis* (*trompe*). Larvae of gadfly are found in reindeer year-round. The presence of a large number of larvae of nasopharyngeal gadfly renders food intake and respiration difficult and running ability is thereby reduced (Crisler, 1956). When the larvae enter the lungs, aspirative pneumonia sets in which usually causes the death of the host. When the larvae of skin gadflies are numerous, emaciation occurs and ulcers and fistulas develop on the skin (the larvae of flies *Phormia terrae novae* later parasitize these wounds). When gadflies are excessive, as happens in a warm summer, the normal grazing regime of reindeer is disturbed. The animals fear gadflies more than other blood-sucking flies and, when the former appear, keep on the move. Emaciated reindeer are the first to die or fall prey to predators in the event of a severe and snowy winter. The mass flight of gadflies promotes the spread of necrobacillosis among hooved animals (Grunin, 1957; and others).

Wild reindeer are infected with skin and nasopharyngeal gadflies to a far lesser extent than domesticated animals. This is because wild reindeer live in summer in small groups or singly, are not restricted in movement, and are free to select areas of habitation where not only gadflies are absent but other bloodsucking flies few. In the Altai only 53 larvae of skin gadfly were found among wild reindeer caught in spring (F.D. Shaposhnikov, 1955) versus more than 1,000 in domesticated reindeer living in the north under different conditions. The degree of invasion of individual animals by nasopharyngeal gadflies depends on the growth of the [nasal] vibrissae. Of 14 wild reindeer caught in Sakhalin, 6 possessed well-developed vibrissae and no larvae of gadfly were found in them; in the other 8 the vibrissae were poorly developed and larvae were abundant (Mishin, 1954). The northernmost outskirts of Siberia, especially Taimyr, and also the Arctic islands are almost free of gadflies. In these parts of the range even other blood-sucking flies are comparatively few (at places, they are almost absent) and gadfly is insignificant in the ecology of wild reindeer there.

---

*Not in Literature Cited—Sci Ed.

In the tundras and taigas more to the south blood-sucking insects (gadflies, mosquitoes, simuliid flies, lice, and horseflies) play a very significant role. These pests influence the habitat distribution and wandering of reindeer in the warm season of the year, the daily cycle of activity, well-being, and antler formation (Pleske, 1887), and other aspects of animal biology. They can be extremely significant in the advancement of epizootic diseases (N.P. Naumov, 1933). According to Sokol'nikov (1927) if the summer in the Anadyr basin happens to be warm and less windy, mosquitoes and gadflies do not allow reindeer to rest and domesticated reindeer grow poorly, especially if the preceding winter has been severe. In the event of the next winter being severe many reindeer cannot survive. To what extent the duration of the blood-sucking fly season varies in different years can be judged from nine-year observations in Lapland preserve, where the duration of mosquito swarms ranged from 25 to 65 days (Semenov-Tyan-Shanskii, 1948). In the southern parts of the range ticks and other ectoparasites also pester reindeer.

Instances of death of wild reindeer in snowy and severe winters in forest and mountain forest regions are almost unknown. Only in Khamar-Daban has it been reported (Fetisov, 1955) that a very large number of juvenile animals died time and again in winters of abundant snow. It is difficult to judge from the author's description to what extent his data are reliable.

The situation differs in the northern parts of the range, especially in the Arctic islands, in the far northern tundra, and in regions subject to glaze ice. Instances of mortality, at least in the past when the reindeer population was greater, were not a rarity. In Novaya Zemlya and Severnaya Zemlya and other Arctic islands wild reindeer become extremely emaciated by spring even in winters of normal 354 severity. On Bogicheva Island reindeer dying from emaciation have reportedly been encountered in winter even though glaze ice was absent (Koshkin, 1937). In years of glaze ice mortality is often high (western parts of the Soviet Arctic, including Novaya Zemlya, and northeastern parts of the country, i.e., Chukotka and the lower Anadyr). Hunters who had spent seven years on Novaya Zemlya reported that during two winters wild reindeer died from hunger in groups of two to five animals at one place; others, barely able to move their legs, vainly attempted to dig the ice crust with their hooves (Krivosheya, 1884). In the winter of 1899 to 1900 reindeer, emaciated and weakened due to prolonged glazes, died over a distance of 100 km to the north of Matochkin Shar on the eastern coast of Novaya Zemlya (Zhitkov and Buturlin, 1901). In the winter of 1917 to 1918 (according to other data, 1920 to 1921), at a time of glaze ice, extensive disorderly wanderings occurred among reindeer in Novaya Zemlya. Some of the animals died on the islands and others moved off onto the ice of the Kara Sea. Fawns were few in spring (Sokolov, 1933; Zubkov, 1935). In the mid-1940's there were up to 300 to 400 wild reindeer on the northern island of Novaya Zemlya; almost all died during a period of glaze ice in 1948 (S.M. Uspenskii).

In 1924 the Dmitri Laptev Strait remained unfrozen until January of the following year, as a result of which wild reindeer, which usually move away in winter onto the mainland, were compelled to remain on the New Siberian Islands where glaze ice commences from autumn. In that winter 4,000 to 5,000 reindeer died on Novosibirsk Island (almost the entire local population; subsequently reindeer resettled). Reindeer mortality also occurred on Faddeyev Island and partly on Kotel'nyi Island (Pinegin, 1932). In 1935 the Lyakhovskiy Islands were mostly covered by glaze ice and again reindeer mortality was seen (Skalon, 1940). Fawns suffer most during glaze ice and dense and deep snow (Aleksandrova, 1937; Mauzan, 1957).

Instances are known when reindeer died in significant numbers while attempting to cross unstable autumn ice or swimming through open straits late in the year (Pinegin, 1932 and Skalon, 1940). Cases have been described, where Chukchis [native people of Chukotka] found innumerable bodies of drowned reindeer on the northern seacoast (D'yachkov, 1893).

Aspects of intraspecific competition among wild reindeer have also not been studied. The most obvious manifestation is combats among males during the period of rut, sometimes ending in injuries and, occasionally, even in the death of one of the combatants. Among domesticated reindeer living in congested conditions competition for food is distinctly manifested and has been detailed by Igoshina and Florovskaya (1939). The main competitor of wild reindeer is its domesticated cousin. The population rise of the latter is almost invariably accompanied by a population reduction, and sometimes even the total disappearance of wild reindeer. In addition to direct persecution by man, competition for winter pastures plays no small role in the population reduction of wild reindeer, all the more so since disorderly grazing and a high utilization of pastures by domesticated reindeer herds damage the reindeer moss cover. It often takes 20 or more years for the restoration of moss and in some cases the damage is irreparable. However great be their population, wild reindeer cannot graze in congested conditions as do their domesticated counterparts. Grazing wild animals are usually extremely mobile and do not graze for long at any one spot. They therefore damage the reindeer moss cover to a lesser extent than domesticated animals (Semenov-Tyan-Shanskii, 1948).

In forests poor in terrestrial lichens competition between wild reindeer and elk favors the latter; elk are well adapted to feeding on arboreal foods, which is not true of reindeer. Thanks, too, to their tall stature elk can utilize arboreal lichens at a height inaccessible to reindeer. When reindeer moss is abundant in the forest, there is no competition between these species. In Kronots preserve wild reindeer visit the winter pastures of mountain sheep only rarely; usually reindeer graze at lower elevations (Averin, 1948). When the lemming population is high, the food productivity of reindeer moss pastures is reduced (Sdobnikov, 1935; Semenov-Tyan-Shanskii, 1948; Tikhomirov, 1955); nevertheless, the role of lemmings as competitors of reindeer is hardly significant. In Yamal domesticated reindeer dig up the stores of Middendorff's voles (at the end of August they contain up to a few kilograms of root stock) and consume them greedily (Dunaeva, 1948).

Tundra [=rock] ptarmigan [*Lagopus mutus*] (Kola Peninsula, Taimyr, Yakutia, and elsewhere) feed in winter on grass seeds and the like in places where the snow has just been dug up by reindeer and it is easy to forage in it (when the snow has frozen these birds are attracted to such places far more rarely). Ptarmigan have very little fear of reindeer and stay in their immediate proximity, sometimes right by their legs (Semenov-Tyan-Shanskii, 1948; and others). White [willow] ptarmigan [*L. lagopus*] in the New Siberian Islands behave in a similar manner (Birulya, 1905; and others).

Some idea of the composition of a wild reindeer population in a territory where the animals are not an object of hunting and wolves are absent,[365] is provided by visual counts made in Lapland preserve (Semenov-Tyan-Shanskii, 1948). In September–October of 1937 and 1938 herds comprised the following:

Fawns of their first year	31%
Females (adults and two-year-olds)	49%
Adult males	10%
Two-year-old males	7%
Domesticated reindeer attached to wild ones	3%

In April of 1936, 1937 and 1938 the herd composition was as follows (counting was done by a different method and hence not all of the data are comparable):

Fawns in their first year	23%
Adult females	39%
Adult males	14%
Two-year-old males and females	20%
Domesticated reindeer attached to wild ones	4%

At the end of winter the number of 11-month-old fawns comprised 59% and of juveniles in the second year 53% of the total number of adult females. As far as the number of fawns is concerned, wild reindeer of Lapland preserve are not inferior to their domesticated cousins (in Alaska fawns constitute an average of 50 to 60% of the total number of adult females and only under extremely satisfactory living conditions 70, or even 85 to 90%; Palmer, 1934).

On Belyi Island near Yamal, where reindeer are objects of hunting occasionally and wolves present, the composition of their population in October, 1935 (Tyulin, 1938) was as follows (method of counting different from that used in Lapland preserve)[366]:

Fawns in their first year	21%
Adult females	46%
Adult males	12%
Two-year-old males and females	21%

Compared with the autumn population composition in Lapland preserve, the percentage of fawns in Belyi Island is low (21 versus 31%); this could be associated with the extreme severity of local conditions and the presence of wolves. In Altai preserve where wolves are numerous fawns in the wild reindeer population constitute up to 20% (F.D. Shaposhnikov, 1955). A similar proportion of juveniles (20%) has been recorded for wild reindeer herds migrating southward along Lake Taimyr (Sdobnikov, 1958).

---

[365] Wolves were seen within the preserve only in the winter of 1939 to 1940.

[366] The figures given were calculated by Druri.

In every instance where the population composition of wild reindeer has been determined (Lapland preserve, Belyi Island, and Taimyr), adult males were considerably fewer than females. In Lapland preserve males constitute 26% and on Belyi Island 21% of adult animals. 356 It has been established on the basis of extensive data for domesticated reindeer that the sex ratio at birth is usually close to 1 : 1, more often with a very slight predominance of males (Druri, 1949). The higher mortality of males may be regarded as the consequence of extremely intense competition for females (Semenov-Tyan-Shanskii, 1948).

A quantitative check at the end of winter carried out over several years in Lapland preserve revealed that from about 100 wild reindeer in 1929, the population had risen by 1940 to 942—an average increase of 23% over a period of 11 years[367]; annual herd mortality averaged 5%, rising to 7% on the arrival of wolves (Semenov-Tyan-Shanskii, 1948).

Periodic (with a 20-year cycle) or occasional (which is more likely) population fluctuations of wild reindeer have been noted in different regions of the country (central section of the European part of the USSR, Kola Peninsula, Nizhnyaya Tunguska and Kolyma, and Yana-Indigirka tundra) (Turkin and Satunin, 1902; Kreps, 1928; Shmit, 1930; Molodykh, 1931; Naumov, 1934; Mikhel', 1937; and others). For want of specific data, it is difficult to judge the nature of these fluctuations.

Field characteristics. Reindeer are much smaller than maral and izubr, and also differ notably from other deer in antler structure (see the general description of these animals). Antlers are present in both sexes (females for much of the year and adult males in winter are without antlers), but in many females in the Altai and Sayans antlers are underdeveloped or absent altogether (see "Growth, Development, and Molt"). Female antlers are smaller and thinner than those of males; females are also slightly smaller in size. In winter older males sport a large mane on the lower part of the neck, which is poorly developed in juveniles.

---

[367] For the period 1902 to 1921 in Alaska the average was 33% among domesticated reindeer after due allowance for animals killed.

A herd of domesticated reindeer differs from that of wild animals in diversity of coloration; white, gray, skewbald, etc. animals are encountered in the former while coloration is uniform, mostly grayish-brown in the latter. In winter tundra wild reindeer are often more light-colored than domesticated ones. Domesticated reindeer usually have a mark in the form of a cut-outs or incisions on one or both ears.

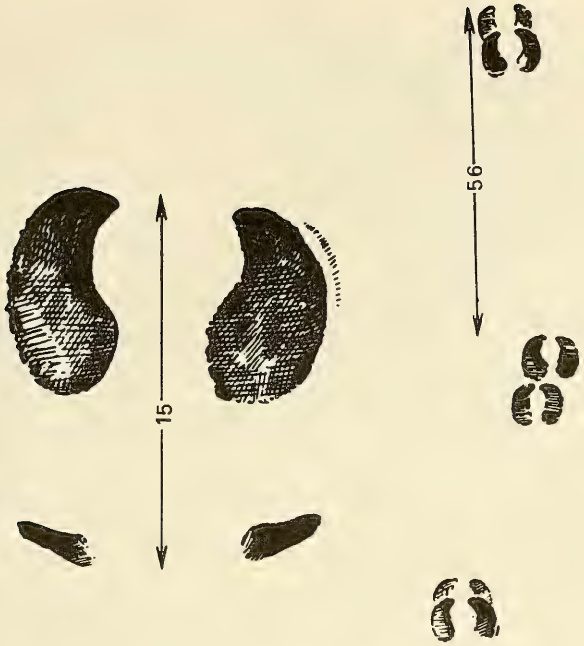
The hoofprints of the two middle digits are reniform and greatly rounded; on soft ground (loose snow and marsh) they are greatly spread apart. The impression of the tiny hooves of the lateral digits is also distinct. On hard ground the edges of the hooves of the middle digits almost fuse into a semicircle. The hoofprint of these digits in a large male is 15 cm long, in an adult female 11 cm, and in a fawn 5 cm. Reindeer rarely gallop, and more often trot or pace. The stride when moving slowly is 50 to 70 cm and when trotting 120 cm (60 cm in fawns). The feces of reindeer are only slightly larger than those of roe deer; often, the former are highly flattened at one end and even a depression sometimes forms.

357 The presence of reindeer can also be deduced from well-beaten trails. They are mainly formed by reindeer running from one place to another to rescue themselves from blood-sucking flies. Hence the trail usually leads to no definite destination and is soon lost, with another appearing somewhere else. Pathways often intersected and the path width is 25 to 30 cm. When a reindeer cleans its antlers, it breaks or damages small pines and other trees and bushes. In summer pasture grounds reindeer moss preserves the tracks of the animals and many tiny shrubs are found uprooted. In winter one notices "pits" dug in the snow and small moss bits on the snow surface; such areas extend long distances.

The call of reindeer, except during the period of rut when males emit a characteristic snore that is audible for 200 m, is heard only rarely. In summer females call to their fawns in a dull low chorus. Fawns respond "mutely" and can be heard only at close quarters. Frightened reindeer emit a sound which can be transcribed as "phoooooo". (A.N.)

Economic Importance

Among the products obtained from wild reindeer, meat and hide are of utmost value. The taste of reindeer meat is inferior to that of elk and maral and best in autumn before the commencement of rut, i.e.,



356 Fig. 112. Hoofprints of reindeer (reduced). Kola Peninsula. June, 1939 (from Formozov, 1952).

in August and September. In the period of rut its edibility is poor and later it becomes very lean. Females lag behind in body growth until mid-winter. The maximum yield of meat may reach 120 to 130 kg[368] (Altai, Sayans, and Kamchatka), but is often much less—60 to 80 kg (10 to 12 kg less in the case of females). In males in autumn the fat layer in the croup builds up to 8 cm (Averin, 1948; F.D. Shaposhnikov, 1955). A male killed in September in Kamchatka yielded 12 kg of subcutaneous fat and over 5 kg of internal (Averin, 1948). Apart from its use in food the fat is suitable for making superior varieties of soap.

Formerly the hides of fawns aged four to six months and up to one year were used as furs. Hides of adult reindeer are inferior as furs because of the brittleness of the hair and are often utilized for chamois. The hunting of juveniles is now prohibited (everywhere in summer). Hides of fawns four months up to a year old are sewn by local people into bags, parkas with fur inside or out and mittens, coats, caps, and so on; hides of adult animals are used for beds

---

[368] But not 190 kg as erroneously stated by Solov'ev (1921).

(beddings, rugs, and so on), sleeping bags (inferior in quality to those made from hides of mountain sheep), harnesses, and coverings for tents. The hide stripped from the legs is used in edging sledges, bags, winter boots, and gloves. Chamois is coverted into summer dresses and sometimes summer boots. Formerly the waste material (wool) obtained during the making of chamois was also used for filling saddle seats. Reindeer hides are best at the commencement of winter, but particularly in autumn; in summer, except in the Arctic they are sometimes spoiled by gadfly larvae.

Reindeer antlers are utilized in various types of articles but are very fragile because of their porosity and brittleness. Tendons were formerly used as coarse threads. Some northern tribes consume not only the meat but also the blood of reindeer (antiscorbutic source); semi-cooked stomach contents are considered a delicacy (Solov'ev, 1922; and others).

In the nineteenth century the catch of wild reindeer in some particularly favorable hunting years probably reached a few hundred thousand animals; such slaughter played a prominent role in the destruction of this species.

According to data from pripolar records for 1926 to 1927, the annual catch of wild reindeer in the Far North was 55,569 animals, including those in former Bulunsk okrug (23,006), Verkhoyansk (15,936), Krasnoyarsk (7,741), Kolyma (3,758), and Tobol'sk (2,063); in other polar regions the catch was much smaller. Taking into
358 consideration reindeer hunting in regions outside the Far North, and also allowing for the probable underestimation of the extent of hunting in the North, the overall annual catch of wild reindeer in the USSR in the period under discussion constituted not less than 70,000 to 80,000 animals. Marketability was very low, i.e., 7.8% (only in the Tobol'sk okrug did it reach 35%).

In subsequent years wild reindeer long continued as important hunting animals in northeastern Yakutia and Taimyr. In the mid-1930's in the tundra west of the Indigirka and in the Tes-Khayakhtakh range, Evenks regarded a year as unsatisfactory if only about 15 to 20 reindeer were caught per family; a catch of roughly 40 animals was regarded as normal; successful families collected up to 150 animals (Mikhel', 1937). In the early 1930's about 500 reindeer were caught annually in the Bol'shoi and Malyi Lyakhovskiy Islands (Pinegin, 1932).

Methods of catching wild reindeer are extremely diverse. Many are only of historic interest now[369] since reindeer hunting has been banned over much of their range. In the past "spearing while swimming," was practiced during the spring and autumn migrations of tundra reindeer in the lower courses of large Siberian rivers from Taimyr to Anadyr and was exceptionally successful. In the nineteenth century and at places even in the first quarter of the twentieth century, the well-being of some local peoples depended greatly on the success of the hunt. According to Vrangel's description (1841), relating to the 1820's "the period of reindeer crossing through Anyuy represents the most important event of the year. Yukaghirs await the appearance of the animals with the same impatience as agriculturists of other countries do the period of harvesting."

---

[369] For a detailed description of hunting methods see N.P. Naumov (1933) and Druri (1949).

During these hunts hunters formed several groups: those in boats speared swimming reindeer with large knives tied to poles (later, guns were also introduced), while others killed them on the shore, and still others gathered the bodies of killed animals. In one hunt sometimes several thousand reindeer were caught, or 60 to 70 animals per hunter. A significant number of injured animals were lost and many bodies washed away by the stream; because of the abundance, not all of the products gathered were satisfactorily used. Meat was prepared for storage by various methods (Sarychev, 1802; Vrangel, 1841; Maidel', 1894; Sokol'nikov, 1927; and others). Hunting of swimming reindeer was nearly responsible for the catastrophic destruction of the wild reindeer population in many regions of northern Siberia.

In view of the fact that reindeer in some years did not traverse through the same well-known places or moved northward in spring even on the ice, the effectiveness of this method of hunting varied widely in different years. A modification of this method of hunting is the catching of reindeer near the river crossing places by setting up beforehand guide fences made of stakes and stones ("makhovka") over long distances (4 to 6 km); these fences were shaped like a funnel. Reindeer were killed near the point of their exit from the "makhovka", or sometimes caught here in a net. This type of hunt depended mostly on the correct determination of the moment of approach of a large herd and guiding the animals along the fences to the traps.

Hunting swimming reindeer, and also its modification, is no longer done but was often practiced in Yakutia even in the 1930's (Mikhel', 1937). In Taimyr reindeer were caught by this method even in 1946 (Pyasina River; M.A. Anisimov). A properly controlled autumn hunt is wholly permissible,[370] all the more so since it makes selective hunting possible. Without control, this method of hunting can turn into a veritable slaughter.

---

[370] Spring products are of extremely poor quality.

A large number of reindeer were caught in the past with the help of barricades set up for several kilometers in wooded localities lying
359 across in the route of migrating animals. Openings were left in these barricades at trails and pits dug there; loops, traps, and rarely automatic devices were laid in these pits. This method of catching ungulates was particularly widespread in the Urals where reindeer were hunted along with elk and roe deer (Sabaneev, 1872; Turchkov, 1930; and others).

Using pits, loops, etc. in combination with barriers extending for several tens of meters, or even without them, reindeer were also caught outside the routes of their seasonal migrations, i.e., at places through which the animals regularly passed during their daily wanderings. This method prevailed in the Kola Peninsula (Semenov-Tyan-Shanskii, 1948) as well as in Siberia. Such a method of catching ungulates has long been banned as irrational and generally dangerous, but is practiced even now by poachers equipped with cable loops, who sometimes also set up barriers.

A very old method of hunting often used today, especially in Yakutia and the Far East, is hunting with "manchiki"—in which wild reindeer are lured by domesticated animals, either on long tethers or without them. Most often males are used for this purpose and hunting done mainly in the period of rut when wild males lose their caution and go to meet the sham rival. More rarely the "manchiki" are females (Yamal, former Kolyma okrug). Hunting with "manchiki" is quite effective even in winter (here it is better to use several "manchiki" since wild animals approach a group more readily than individual animals) and is wholly permissible at this time of year.[371]

Another old method of hunting sometimes practiced today is winter hunting with a shield. The hunter pushes in front of him a white shield set up on a small sledge or on skis and approaches the reindeer until within shooting range. This type of hunting is possible in the tundras and on gentle forest-free mountains. In forests this method is practiced in combination with tracking down the animal, for which leashed dogs are often used. It is sometimes possible to approach wild reindeer using domesticated reindeer as cover. Such a method of hunting is also practiced in many regions of the country.

---

[371] In the period of rut, however, hunting is undesirable since it adversely affects reproduction.

In general, concealment by various methods is one of the most popular methods of hunting today.

In the Siberian tundras an extremely characteristic method of winter hunting is based on the instinctive urge of wild reindeer to turn leeward when an unknown object approaches. Hunters chasing wild reindeer on dog or reindeer sleighs attempt to stay on the leeward side. A wild reindeer eluding pursuit and attempting also to stay on the leeward side moves in a circle along the arc of a large radius; eventually, however the distance between the hunters and the animal diminishes until the latter falls within shooting range (Druri, 1949). This hunting method requires great skill and is not often employed.

Catching reindeer by lying in wait for them on their trails in places of daily movement is widely practiced. In the taiga one method sometimes used is chasing reindeer into a pen, based on the fact that animals escaping pursuit prefer to run along a path (Sabaneev, 1872). Late winter chasing of animals on deep snow covered with a thin crust sufficient to hold the weight of a skier, but collapsing under the weight of an animal, is largely responsible for the extinction of reindeer in the taiga subzone. Hunters formed groups and chased reindeer in relays, sometimes for two to three days. This method was used to destroy a large number of reindeer in the snowy winter of 1862 to 1863 in the Vitim uplands (Polyakov, 1873). Chasing ungulates on snow and crust, though prohibited, is still practiced rather extensively. Other, more uncommon methods are also used to catch reindeer (for example, methods based on animal "curiosity").

According to a government resolution of November 21, 1956, aimed at regulating the utilization and conservation of the natural
360 resources of the arctic and subarctic regions, catching wild reindeer is permitted only for meeting the needs of the local collectives in the Khanta-Mansiisk, Yamal-Nenets, Taimyr, Evenkia, Chukotka, and Koryak national okrugs,[372] and also the northern regions of Yakutsk Autonomous Soviet Socialist Republic. Wild reindeer hunting is prohibited in other regions of the Far North. In the rest of the range hunting is greatly restricted (by introducing licenses and permit hunts by only small communities of peoples) or totally prohibited. In many parts of the range, including the Arctic islands, wild reindeer should be conserved far more strictly than presently enforced.

---

[372] In the latter two regions almost no efforts have been made to conserve wild reindeer. Adequate measures for their total conservation are urgently needed here and in several Arctic islands.

The suggestion (Druri, 1949) that several game preserves and sanctuaries[373] be established at places of mass wintering of Siberian reindeer in the forest tundra and northern taiga deserves support.

Reindeer hunting should be restricted to September through March and the duration limited to no more than 1.5 to 2.0 months in any given area. Reindeer catching in the period of estrus is best prohibited. Hunting females should be restricted. The maximum norm of hunting should be 5 to 10% of a herd.

Wild reindeer could prosper well in places where domesticated reindeer husbandry is altogether uneconomical for reasons of poor winter pastures and the impossibility of feeding a substantial number of animals. Under such conditions it would be far more advantageous to set up an organization to hunt for wild reindeer; this is particularly applicable for many of the Soviet Arctic islands. Even in other parts of the range this species could represent an object of profitable hunting.

In regions of intense reindeer husbandry wild reindeer are often regarded as undesirable, often without substantiation, since in the periods of migration and estrus, and sometimes even at other periods of the year, domesticated reindeer living under poor conditions escape with wild reindeer herds. Instances are known when 100 to 200 domesticated reindeer have escaped en masse with wild animals (Sokol'nikov, 1927; Mikhel', 1937).

Wild and domesticated reindeer often interbreed; most often wild males mate with domesticated females. The resultant fawns are much stronger, and sometimes more fully developed, but wild. In taiga regions these hybrids are considered undesirable, while in tundra regions, where reindeer have been domesticated to a lesser extent, they are highly valued (Sdobnikov, 1935). On Nunivak Island, close to Alaska, crossing of caribou with domesticated reindeer has been successfully practiced for several years. Hybrids yield far more products than slaughtered domesticated reindeer. (A.N.)

---

[373] For conserving wild reindeer, the preservation of reindeer moss is of particularly great importance. The institution of preserves for reindeer conservation is totally justified even if the animals spend only a part of the year in them.

Superfamily of Hollow-horned Ungulates
Superfamilia BOVOIDEA Simpson, 1931

Family of Hollow-horned Ungulates, or Cattle

Familia BOVIDAE Gray, 1821

361 Ruminants of small, moderate, large, and sometimes very large size. As a result of specialization of different members of the group, the general build is highly varied, from light and slender to heavy and massive.

With a few exceptions, the number of digits is four and the lateral digits carry small hooves with a rudimentary skeleton. Usually they do not function but in some genera (*Rupicapra* and *Kobus*) they play an active role in locomotion under certain conditions. The metacarpals of digits II and V are greatly reduced and only their proximal parts preserved to varying degrees. Usually the metacarpal of digit II fuses with the cannon bone, while the metacarpal rudiment of digit V resembles a splint which is fused with the cannon bone in its proximal part. The metacarpal rudiment of digit I is preserved, exceptionally. The distal rudimentary parts of the metacarpals of digits II and V occur on the lateral sides of the hooves in the form of tiny bones of indefinite form. The metatarsals of digits II and V are reduced to a greater extent than the corresponding metacarpals and almost wholly fuse with the metatarsals of digits III and IV. Only one or two of the phalanges of digits II and V, which form the skeleton of the lateral digits, are preserved; sometimes they are altogether absent.

The basiocranial axis is highly flexed, i.e., the cranial part of the skull is set at an angle to the facial part. Due to this and the growth of horns, the parietals are pushed markedly into the occipital region of the skull and a considerable part of the skull is formed by the frontals, which cover most of the skull roof. The facial part of the lacrimal is highly developed and with or without a pit for the preorbital gland. The orbital region of the lacrimal has a single lacrimal foramen along the inner rim. The ethmoid pit is absent, weakly developed, or, rarely, well developed. Depending largely on the development of this pit, the facial part of the lacrimal usually abuts the nasal bone. The maxilla usually extends markedly onto the facial part of the skull. Pneumatization of the skull is prominent in most members and, when developed to the maximum extent (cattle) involves most of the bones, but sometimes pneumatization is weak.

The premaxilla is relatively small, its nasal process small, and only in rare cases does it project backward and upward to wedge between the nasals and maxillae, or to wedge between the lacrimal and nasal bones. Tympanum fused with the petrosal and enlarged to varying degrees, sometimes markedly; usually it is hollow inside.

The cheek teeth are usually hypsodont and columnar, i.e., their
362 crowns run into the roots almost without a neck; only exceptionally is the crown demarcated below by a horizontal ridge. The teeth are invariably tetraselenodont. There are no upper canines.[1] Dental formula:

$$\mathrm{i}\,\frac{0}{3},\ \mathrm{c}\,\frac{3}{3},\ \mathrm{pm}\,\frac{3}{3},\ \mathrm{m}\,\frac{3}{3} = 32,$$

or in rare cases, $\mathrm{p}\,\frac{3}{2} = 30$, or even, $\mathrm{p}\,\frac{2}{2} = 28$.

Horns are invariably present in males and are also characteristic of most females but usually somewhat smaller. In some species females are devoid of horns. Horns two, but in one case four (Indian fourhorned antelope [chousingha] *Tetraceros*). The horns consist of corneous matter of epidermal origin and are hollow inside with a bony, usually highly pneumatized, core at the base inside, sometimes almost throughout the horn length and representing the apophysis of the frontal bone (part of the core is formed as an independent os cornu). The horns are extremely varied in form, position, and size, but never branched; they grow continuously and are not shed. In a very large number of cases the horns are twisted and more or less spiraled; furthermore, the right horn may be twisted rightward and the left leftward (homonymous horns) or vice versa (heteronymous). Knobs, transverse folds, and rings, or longitudinal ribs are often seen on the horns. The horn cross section is circular, oval, or triangular.

The scent glands are highly developed (much more so than in Cervidae) and are often lodged in saccate invaginations. They are distributed on the facial part of the head, in front of the eyes, on the occiput, on the back (in the form of longitudinal folds), at the base of the tail, on the groins, the lower part of the limbs, between the hooves, and on other body parts. Some glands exude a very strong odor (caudal glands in goats), while others exude a weaker scent. These glands are associated either with reproductive activity (usually better developed in males) or with social life in herds, characteristic of nearly all members of the family (odorous tracks on grass or ground), or with territorial delineation.

---

[1] Canines form but do not emerge. They are functional only in dwarf antelope (*Madoqua*).

The hair coat is extremely diverse, from long, shaggy wool to short, close hair. The color of adults ranges from pure white to almost black: coloration is usually fairly uniform without sharply contrasting patterns (which, however, often occur on the head) and sometimes cryptic (usually yellow shades). In several species a bright-colored patch (speculum) occurs in the rear, on the rump. Sexual dimorphism is usually insignificant and manifest in the above-discussed growth characteristics of horns and in minor size differences (males usually larger but sometimes vice versa), which are sometimes prominent (*Boselaphus* and some others). Age-related changes prominent. Gall bladder present in almost all species. Placenta with numerous cotyledons. Teats two or four.

Unlike deer (not to speak of families with a smaller number of species), Bovidae represent an extremely diverse group, many members of which widely differ from each other in general appearance, build, and other individual features. Bovidae are the most heterogeneous group of all "ungulates". The family includes heavy and massive, short-legged cattle, very light, long-legged gazelle, relatively heavy and large "antelopes"[2] such as eland and oryx of com-
364 pact build, moderate-sized goats and sheep, and dwarf antelopes. Horn structure varies widely, from long, thin, lanceolate shapes set almost vertically to short, thick forms set sideways and downward. Size is likewise highly diverse. The largest form stands almost 200 cm at the shoulders and weighs up to 1,000 kg (European and American bison); the smallest is the size of a rabbit, reaching about 52 cm at the shoulders and weighing 2 or 3 kg (*Neotragus* and some related genera).

Bovidae constitute an extremely diverse biological group, mostly steppe, semidesert, and desert, often mountain animals. Some spe-

---

[2] The term "antelope," used extensively in literature (even in scientific works and textbooks), is devoid of meaning from the point of view of systematics. This term is used to denote extremely diverse cavicorn ungulates, mostly exotic ones, belonging to diverse subfamilies of Bovidae and different families (pronghorn "antelope" Antilocapridae). In practice, the term "antelope" mostly signifies cavicorns (Bovidae) other than cattle, buffaloes, goats, sheep, and musk ox. Gazelle and some other species (gorals) are also sometimes called "antelopes." In zoology the term "antelope" should be used only for members of the subfamily Antilopinae (see below), i.e., different types of gazelle and dwarf antelope.

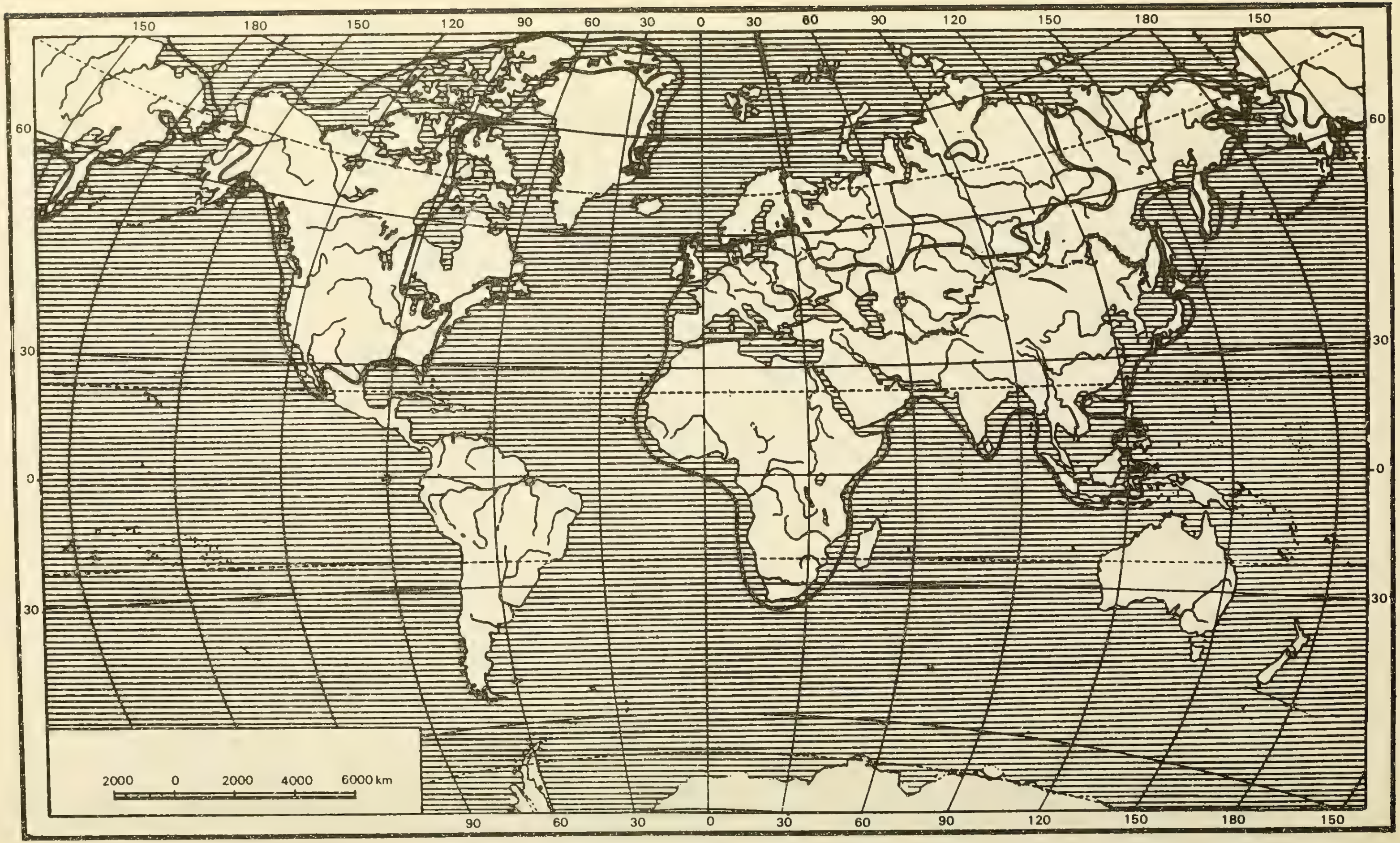

150
180
150
120
90
60
30
0
30
60
90
120
150
180
150
60
30
0
30
2000
0
2000
4000
6000 km

Fig. 113. Geographic range of family Bovidae (reconstructed) (scale in km). V.G.Heptner.

cies are found in different types of forests (mostly tropical and subtropical, absent in the taiga), in swampy fields, and even in the rocky tundra of high Arctic regions (*Ovibos*). In mountains they are scattered right up to the very high altitudes (encountered at altitudes higher than that of almost all other mammals, up to 5,500 m or even more). These species are gregarious and live in fairly large groups, sometimes very large (up to several hundred or even several thousand under certain conditions), or small groups, or even singly as an exception. They are herbivorous and feed almost exclusively on grass.

Bovidae are very widely dispersed. In the Old World, the geographic range covers all of Africa (except Madagascar), western Europe (except England[3]) in the north to the south of the Scandinavian Peninsula and the Gulf of Finland, eastern Europe to the upper Volga, Samarsk Luka, and the southern extremity of the Urals. Beyond the Urals, the range covers southwestern Siberia and much of central and eastern Siberia and the Far East. In southern Asia distribution encompasses India, Ceylon [Sri Lanka], Indo-china, Sumatra, Java (in Bali only the domesticated form of banteng), Sulawesi (Celebes), and Mindoro[4] among the Philippine Islands. In the east the range covers Taiwan (absent in Hainan and evidently never there), Japan (Honshu, Hondo, Shikoku, and Kyushu). These animals are absent in Hokkaido and, evidently, were never there, nor in Sakhalin and Kuril Islands (except in the extreme northern island).

In the New World the reconstructed range covers most of North America (except the northeastern part) in the south to California, Florida, northern Mexico (Chihuahua), the Arctic archipelago, including Grant Land (absent on Baffin Island), the north coast of Greenland and also its southeast coast up to latitude 70° N lat. (Scoresby Sound). This family is not known in the West Indies and Central and South America.

Some species have been acclimatized beyond the limits of their natural range (mouflon and others) and even beyond the family range (chamois, tahr, and *Pseudois* in New Zealand, etc.). The range of many species has shrunk, in some cases very sharply, as a result of reckless persecution by man.

In spite of the number of species and their great diversity Bovidae represent an extremely natural group, distinctly separated from all other families of Ruminantia, especially Cervidae. Family Antilocapridae (pronghorns) exhibits great affinity with Bovidae. Some taxonomists include it in family Bovidae as a special subfamily. In their main structural features pronghorns are no more different than many other members of family Bovidae; only their build and the fact that they shed their horns justify assigning such a high rank to this group. Paleontological material convincingly demonstrates the great antiquity of Antilocapridae from the Middle Miocene in the New World (12 extinct genera known); they evolved parallel to Bovidae, and independently.

---

[3] Members of the family evidently did live there very long ago, in the prehistoric period.

[4] On the other island of the archipelago only some domestic forms which have turned wild are found (buffalo); they are absent on Palawan and Sulu Islands.

Family Bovidae apparently arose from Oligocene Tragulidae. 366 Genera *Archaeomeryx* (Hypertragulidae) and *Gelocus* (Tragulidae) are closest to their probable ancestors (Sokolov, 1953). Typical members of this family, however, began to appear only in the Lower Miocene of Europe. Eurasia represents one center of evolution of the group although Bovidae are known in Asia only from the Lower Pliocene.[5] In Africa, the present-day center of their maximum evolution, they appeared only in the Lower Pliocene and in North America, where Antilocapridae are known to have prospered, a few members of Bovidae colonized only in the Pliocene. Representatives of Bovidae were never present in South America.

Having proliferated rapidly, Bovidae flourished well throughout the Upper Tertiary period when they generally constituted a rich, diverse, and prolific group of ungulates. Being a recent group, Bovidae are characterized by the absence of extinct subfamilies.

Bovidae are a flourishing group of ungulates today. In number of species they exceed all other "ungulates" taken together. The sharp elimination of many species and the drastic reduction of their geographic range in the Recent period are more the result of direct and less of indirect destructive human activity, to which all large mammals are exposed.

The systematics of the family are extremely confused. This is due, firstly, to the abundance and diversity of species constituting the family, and secondly since cavicorns were the object of systematic studies over 200 years, to the very large number of zoologists and paleontologists who based their studies on extremely diverse parameters, which were not always well substantiated. This is particularly true of the supraspecific classification. At present all researchers recognize, in principle, the broad outline of the family adopted here. In the past, however, almost every group of genera,

---

[5] Quite likely from the Lower Miocene (Mongolia; Sokolov, 1953).

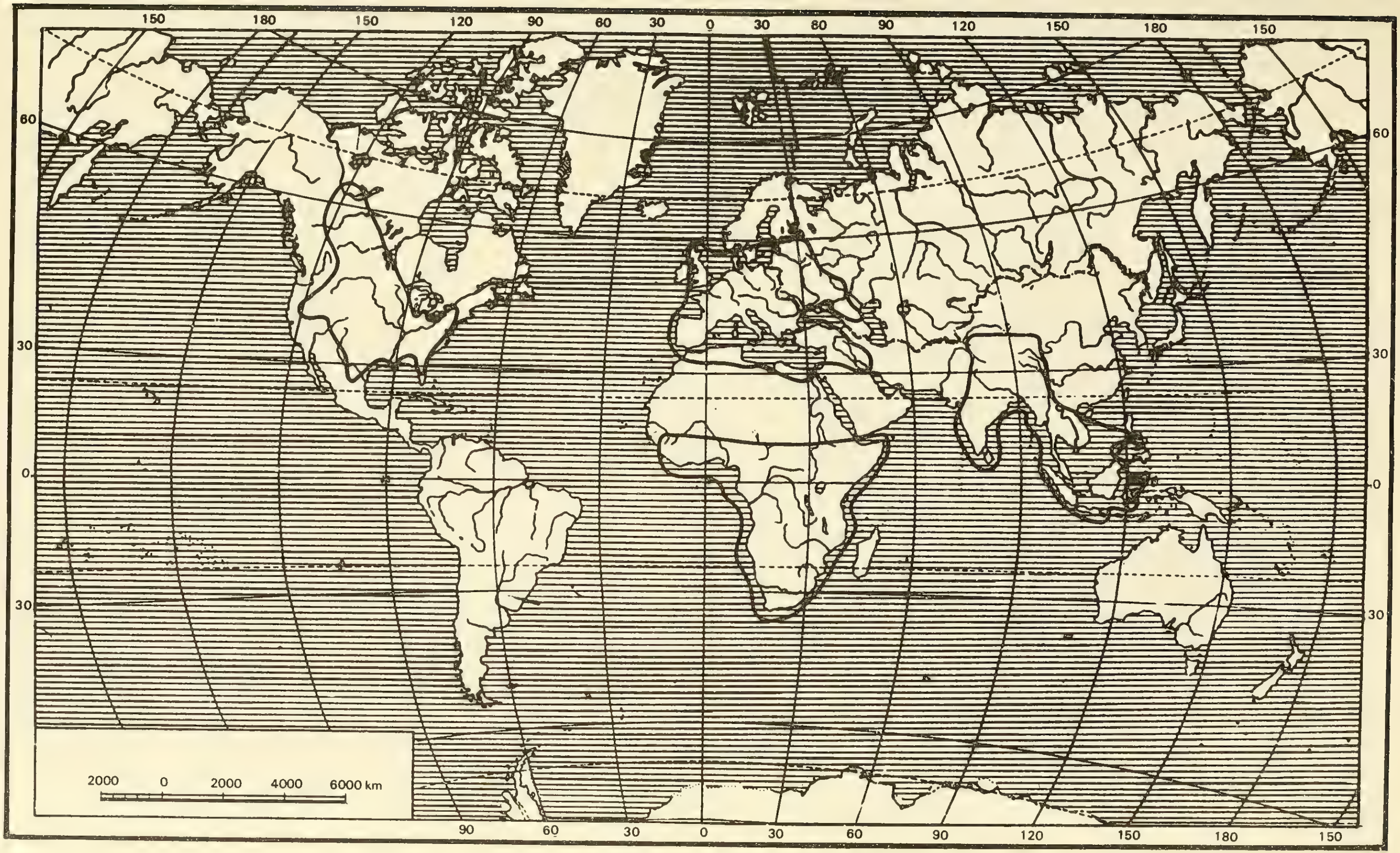

150
180
150
120
90
60
30
0
30
60
90
120
150
180
150
60
30
0
30
2000
0
2000
4000
6000 km

Fig. 114. Reconstructed geographic range of subfamily Bovinae (scale in km). V.G. Heptner.

whether slightly or sharply deviating from the rest, was regarded as a distinct family. In general, 15 to 20 such families were established.

The number of subfamilies in the family acknowledged by various researchers also varies widely—from 3 to 5 (Simpson, 1945), 6 (Sokolov, 1953), 13 (Weber, 1928), and even 16 (Lydekker, 1913 and 1914). Even more inconclusive are concepts about certain genera and the number and delimitation of species; in many groups these are being gradually elucidated only now.[6] In spite of significant success in elucidating the taxonomy of cavicorns in recent years, our concepts cannot as yet be considered totally clarified, primarily in relation to supraspecific groupings and species composition. In spite of their great variability Bovidae species can be considered a distinctly separate group from the contemporary point of view.

It would be most natural to divide the family into five subfamilies (all extant): Bovinae (true cattle), Cephalophinae (crested antelope; 3 genera in Africa), Hippotraginae (oryx; 13 genera in Africa), Antilopinae (gazelle and dwarf antelope), and Caprinae (saiga, chamois, goral, musk ox, goats, and sheep). There are 140 genera in the family (54.5% of all genera of Ruminantia); 86 are fossil and 54 contemporary (about 72% of present-day genera of ruminants).

In number of species Bovidae represent an extremely extensive family of the suborder Ruminantia and of the order as a whole; the number of species of cavicorns is more than the number of species of all the remaining families of the order taken together. Until recently cavicorns supposedly comprised about 200 species. In fact, they comprise only 106, i.e., 70% of all ruminants (Ruminantia) or 64% of Artiodactyla. The largest number of species inhabit Africa (66); 32 are Eurasian, 6 African and Eurasian, 3 North American, and 1 Eurasian and American.

367 Bovidae are important game animals hunted mainly for their meat, often for their hide, and to a lesser extent for their horns (for making articles and as pharmaceutical material). Almost all the species serve as objects of sport, which in some regions is organized on a very extensive scale (eastern Africa). Some species damage crops. Many species constitute a source for trypanosomiasis of man and domestic animals (Africa).

The most important domestic animals are cavicorns and most are also found in a wild state [sheep, goats, and some cattle (gaur;

---

[6] In the case of one or two species of mountain sheep of Eurasia, older researchers delineated 6 to 17 species and some placed the various races of the same species (in terms of modern concepts) even in different genera. The number of species of African forms has been sharply reduced.

gayal)]. Along with forms which differ markedly from their wild ancestors, one finds some which are still in the early stages of domestication and turn wild easily. In ancient Egypt some species of "antelopes," including oryx, were raised as domestic or semidomestic animals; these animals now exist only in a wild state.

As a result of thoughtless persecution, the geographic range and population size of most species have shrunk, in some cases dramatically. Some species have become totally extinct. Some species are now legally protected and most are under partial or total protection. To eradicate trypanosomiasis a systematic destruction of cavicorns is practiced at some places in Africa. Some species are acclimatized in foreign countries for hunting purposes (Europe and New Zealand).

The Russian fauna includes three subfamilies—Bovinae, Antilopinae, and Caprinae (60% of all the subfamilies), 8 genera (about 15%), and 12 species (about 8% of species of the family).

Russian representatives of the family inhabit the steppes, deserts, and the mountains of the Caucasus, Middle Asia, eastern and partly northern Siberia, and the Amur-Ussuri region.

Throughout history the population size and range of all species have undergone significant changes, often dramatic. All species are protected fully or partly by local laws; one species (goral) is given total protection, while another (European bison), inhabiting the western and southern parts of the USSR and the Caucasus is no longer found in a natural state; it is raised in special nurseries and preserves. One or two species have become extinct such as aurochs*, which inhabited the western regions of the USSR and became extinct by the seventeenth century, and wild yak which possibly survived in the historic past in Siberia (even before the eighteenth century ?).

These are game animals valued for their meat and hide (mainly for local consumption). One species (saiga) was raised on a large scale in the pre-Revolution period for its antlers, which were exported to China for pharmaceutical purposes. (V.H.)

Key for Identification of Species in the Family Bovidae

The key given here includes all the Russian wild species of the family except the extinct aurochs and wild yak. Apart from the species described here, three domesticated species are also found in

---

*Here and elsewhere Heptner seems to have used the same Russian common name (tur) for both "aurochs" and "tur". Aurochs (*Bos primigenius*) became extinct in 1627, whereas tur are still flourishing—General Editor.

the Soviet Union. These are large horned cattle ("*Bos taurus*"), descendants of aurochs (*Bos primigenius*), described below and raised almost throughout the USSR; domesticated yak "*Bos* (*Poëphagus*) *grunniens*", descendants of wild yak *Bos (Poëphagus) mutus* which are seen in Pamir and in some adjoining regions of Middle Asia and the Altai; and the Indian buffalo ("*Bubalus bubalis*") raised in the Caucasus, representing the domesticated form of the Indian wild buffalo (*Bubalus arnee*). In some regions where yak are raised hybrids between yak and domestic cow occur. For these well-known animals as also for wisent or European bison (*Bison bonasus*), the status of which has not yet been defined, only some craniological characteristics have been given at the end of the key. Sometimes it is necessary to differentiate their skulls.

368 1 (2). General appearance that of a bull or a cow and size not less than that of domestic cow. Maximum skull length exceeds 42 cm . . . . See character 25 below. (pg. 531)

2 (1). General appearance different and size much smaller. Maximum skull length less than 42 cm.

3 (4). Snout very large, as though highly swollen, and overhangs mouth in the form of a short, thick proboscis; downwardly directed circular nostrils open at the end. Anterior nasal openings of skull very large. Nasals very short (width of each bone roughly equal to half its length) and their anterior margins set straight forward or slightly upward. Lacrimal very large, its rim forming a significant part of the wall of nasal passage between nasal and maxillae (these two do not come into contact and lacrimal segment between them not less than one-half diameter of orbit). Nasal processes of premaxillae extend just a little beyond posterior margin of infraorbital foramina . . . . saiga, **Saiga tatarica** L. (pg. 662)

4 (3). Snout of normal dimensions, not swollen, and does not overhang mouth in the form of a proboscis. Anterior nasal opening of normal size; nasals long (width of each bone less than one-half its length) and their ends set forward and downward. Lacrimal of normal size and does not form part of lateral wall of nasal passage (maxillae touch nasals or are separated from nasal segment by lacrimal, the length of which is less than one-half diameter of orbit). Nasal processes of premaxillae extend far behind posterior margin of infraorbital foramina, sometimes extending up to nasal bones or even wedging between nasal and maxillary bones.

5 (6). Tail bicolored; greater part sandy-yellow and an extension of color of back, and terminal part black. Rear of rump with

large white speculum bounded by a black band on sides. Horns thin, lyrate, and black in color. Anterior free margin of nasals deeply notched all along width of bone . . . .
. . . . dzheiran, **Gazella subgutturosa** Gueld. (pg. 608)

6 (5). Tail unicolored—white—or else corresponds to general color of back. Speculum absent or not bounded by a black band on sides. Horns differ in form and size. Notching absent on anterior margin of nasals.

7 (8). Tail white, with large speculum reaching far above base of tail. Horns lyrate, very thin (their diameter at base roughly corresponds to diameter of orbit), circular in cross section, with distinct, large, transverse annular prominences at base, but smooth at terminal part. Forehead at junction of frontal and nasal bones strongly convex, length of nasals exceeds shortest distance between outer margins of orbit . . . .
. . . . dzeren, **Procapra gutturosa** Pall. (pg. 636)

8 (7). Tail not white and speculum absent, or does not extend above base of tail. Horns not lyrate. Forehead at junction of frontal and nasal bones not convex, sometimes even concave; length of nasal bones less than shortest distance between outer margins of orbit.

9 (12). Horns thin (their diameter at base less than diameter of orbit or equal to it), circular in cross section throughout, smooth, without longitudinal ridges, faces, knobs, or circular, transverse annular prominences at base (a small wrinkle may occur at base). Nasal processes of premaxillae do not reach nasals. Females sport horns of the same form and size as those of males and have four well-developed teats.

369 10 (11). Horns directed backward and continue the line of the forehead-nasal profile; they are short, invariably shorter than skull, sharp, and straight (terminal portion slightly bent downward). Nasals short, narrow anteriorly, greatly enlarged posteriorly, in contact only with the frontals and come close to lacrimals over a very small section (no contact with maxillae[7]). Tail together with terminal hair considerably longer than ear; reaches or almost reaches hock . . . .
. . . . goral, **Nemorhaedus goral** Hardw. (pg. 703)

11 (10). Horns set vertically and their ends turned backward and downward like a hook. Nasals relatively long with no sharp difference in width of anterior and posterior ends. Nasals fuse

---

[7] Sometimes lacrimal reaches edge of nasal aperture; however, the position found in character 3 (4) never arises.

with frontal and lacrimal bones and also with maxillae over much of their length. Tail together with hair shorter than ear or equal to it; falls far short of hock .... serna, **Rupicapra rupicapra** Linn. (pg. 723)

12 (9). Horns of male thick (their diameter at base greater than diameter of orbit), not circular in cross section or only irregularly so at base, and flattened at tips; knobs, transverse ridges, coarse transverse folds, longitudinal ridges, and flutes visible on surface. Nasal processes of premaxillae reach or almost reach nasals and sometimes are wedged between nasal and maxilla. Females without horns or have very small horns, which are considerably smaller than those of males. Females have two fully developed teats and two rudimentary teats posterior to them.[8]

13 (22). Horns dark (black or grayish-black). Well-developed beard on chin in the form of a wedge-shaped tassel of long hair.[9] Preorbital glands absent. Hoof glands absent on hind limbs. Glands present on under surface of tail which exude a sharp goaty smell. Tail with hair at end longer than ear. Lacrimal depression ("tear hole") and linear ridges on lacrimals absent. Nasal processes of premaxillae wedged between nasals and maxillae. Coronary suture usually fairly straight and does not jut forward at an angle .... genus of wild goats, Genus **Capra.** (pg. 748)

14 (15). Horns flattened, spirally twisted (screw-shaped) and directed upward.[10] In addition to beard on chin, mane of long hair occurs on throat and chest .... twisted-horn goat, **Capra falconeri** Wagn. (pg. 859)

15 (14). Horns of a different pattern. No mane on throat and chest.

16 (17). Anterior surface of horns in the form of a sharp ridge with many sharp, longitudinal prominences projecting from it .... bezoar goat, **Capra aegagrus** Erxl. (pg. 756)

---

[8] Identification of females of species falling in this category is difficult from this key. In most cases females of goats and sheep are easily identifiable by their general appearance. In others, however, their identification should be based on males with an emphasis on distribution: in each area only one species of sheep and one of goats are distributed. Exceptions are some parts of the Great Caucasus (see later). Descriptions of this particular species should be relied on in identifying the rest. This partly applies to young males (up to a year or slightly older).

[9] In one case the horn is black, but the beard absent. Furthermore, the color of the animal is brownish and a large white spot occurs on the side. This is a form of sheep—mouflon (*Ovis ammon musimon*)—found in the Soviet Union only in Crimean preserve (acclimatized Corsican and Sardinian forms).

[10] Horns of female also exhibit a tendency to twist; in this respect these horns differ from those of all other goats.

17 (16). Anterior surface of horns not in the form of a sharp ridge.

18 (19). Cross section of horns at base distinctly triangular; anterior surface flat, sharply set off from lateral surfaces, with regular rows of prominently projecting transverse ridges throughout their length (except at the very tip) .... Siberian ibex, **Capra sibirica** Pall. (pg. 774)

19 (18). Cross section of horns at base fairly circular; horns flat at tip and without sharp longitudinal ridges on anterior surface. Transverse rows of prominently projecting ridges absent; a few fairly sharp wrinkles occur or fairly prominent transverse rows of not sharp ridges seen only in basal part of horn.

20 (21). Horns falciform, in one plane or almost so; transverse knots may be present on anterior surface at base .... Kuban tur, **Capra caucasica** Gueld. and Pall. (pg. 816)

21 (20). Horns bent in several planes and represent the initial stage of a very broadly opened-up spiral; they are directed initially upward, backward, and sideways, and later, inward and slightly downward; at the very end, inward (toward the neck) or inward and slightly upward. Terminal part of horns thus turned toward each other over the neck.................. .... Dagestan tur, **Capra cylindricornis** Blyth. (pg. 826)

22 (13). Horns light-colored (yellow). No beard on chin (but a mane on throat, lower part of neck, and chest is possible). Preorbital glands present. Hoof glands present on hind limbs. Glands on under surface of tail exuding goaty smell absent. Tail with terminal hair shorter than ears. Lacrimal depression ("tear hole") and linear ridges on lacrimals well developed. Nasal processes of premaxillae not wedged between nasals and maxillae. Coronary suture usually juts forward at an angle (upward) .... genus of wild sheep, Genus **Ovis.** (pg. 874)

23 (24) Height of bony horn pedicels on skull more than circumference at base. Length of nasals more than one-third maximum length of skull...... arkhar, **Ovis ammon** Linn. (pg. 881)

24 (23). Height of bony horn pedicels on skull less than circumference at base. Length of nasals less than one-third maximum length of skull................................. .... snow sheep, **Ovis canadensis** Shaw. (pg. 954)

25 (26). Vomer fused with palatine and completely divides posterior nares into two parts—right and left. Horn pedicel triangular in cross section and with three distinct longitudinal ridges. Horn distinctly triangular in cross section, with flat anterior surface, and longitudinal and broad transverse ridges in basal portion. Tops of notch of hard palate lie posterior to line

joining posterior edges of last molars; distance on each side between tops of notch and posterior part of last molar more than length of last molar . . . . Buffalo.

26 (25). Vomer does not fuse with palatine and does not divide posterior nares into two distinct parts. Bony horn pedicel circular in cross section, without distinct longitudinal ridges. Horn circular in cross section and without flat anterior surface or longitudinal and transverse ridges. Tops of notch on hard palate lie posterior to line joining posterior edges of last molars; distance on each side between tops of notch and posterior part of last molar significantly less than length of last molar.

27 (28). Skull relatively short and broad, especially in the frontal region, and orbits project outward prominently. Frontal region of skull convex. Maximum width of skull, measured at 371 level of orbits, about 1.5 times basal length. Skull width behind orbits invariably greater than width at level of zygomatic arch. Crest between horn bases on skull absent . . . . zubr, **Bison bonasus** Linn. (pg. 557)

28 (27). Skull relatively long and narrow, especially in frontal region, and orbital cavity projects outward relatively weakly. Frontal region flat. Maximum width of skull, measured at level of orbits, about twice basal length. Well-developed crest present between horn bases on skull.

29 (30). Crest between horns prominently developed, projects backward, overhangs occipital portion of skull and covers almost all the space between bases of bony horn pedicels. Width of skull behind orbits less than width at level of zygomatic arch. Nasal processes of premaxillae usually reach, or almost reach, nasal bones . . . . Domesticated cattle.

30 (29). Crest between horns relatively weakly developed and covers only midportion of the space between horns. Width of skull behind orbits equal to or greater than width at level of zygomatic arch. Not more than one-quarter of length of nasal processes of premaxillae reaches nasal bones . . . . Yak (pg. 549) (V.H.)

Subfamily Bovinae Gill, 1872 (Cattle)

Large to very large animals, only exceptionally moderate in size, usually heavy and massive in build, often very high at withers, with short, thick neck, and heavy head set low.

Digits II and V* hooved. Vertebrae: C 7, Th 13-14, L 5-7, S 4-5, and Ca 15-18. Spinal processes of thoracic (sometimes also of seventh cervical) vertebrae greatly elongated in several species.

---

*IV in Russian original—Sci. Ed.

Facial part of skull highly developed, but not elongated: frontal bones highly developed (maximum for family) and extend far backward or moderately developed; occipital bone small. Pneumatization of skull maximum or moderate. Preorbital depression on lacrimal absent or poorly developed, rarely well developed. Ethmoid pit usually absent or small. Nasals and premaxillae normal in size, sometimes come close together; nasal opening normal in size.

Dental formula:

$$i\frac{0}{3},\ c\frac{0}{1},\ pm\frac{3}{3},\ m\frac{3}{3} = 32.$$

Upper molars with broad crowns, greatly hypsodont, rarely relatively low; in some genera a small additional cone (metaconule) occurs between two main cones. Incisors broad, decreasing uniformly in width from first incisor to canine; more rarely, anterior pair enlarged in form of an asymmetrical spatula.

Horns two, but four in one species.[11] In some species horns homonymous, smooth or almost so (without significant transverse ridges; some waviness, folds, or "wrinkles" may be present in basal portion), set close to occipital region of skull (on "top of it"), and sometimes widely separated. Horns directed sideways in basal half, later upward and then inward, backward, or forward. Horns massive, especially at base; relatively short or moderate in length and circular in cross section. Sometimes longitudinal ridge, or two or 372 three ridges occur and sometimes cross section at base fairly triangular, and horn more elongated (some cattle). In certain species horn bases close-set and horns usually straight, rather tightly spiraled,[12] heteronymous, totally devoid of transverse ridges, but almost invariably with a longitudinal ridge along anterior surface. Horns usually relatively slender and long, sometimes short and without a spiral bend or twist; exceptionally lyrate, smooth, and straight. Horns black or light in color. In some species females also have horns which are only slightly smaller than those of males; in other species females are devoid of horns.

Muzzle large but not swollen or produced into a proboscis, slightly enlarged, bare, undivided, and usually moist. Compound skin glands poorly developed. Facial glands present in some species but absent in most. Flank glands present in some species but hoof glands absent. Only some species have special glandular areas associated with the lateral hooves of the hind legs. Tail moderate in length, densely and uniformly covered with hair, or with a long tassel at the end. Dewlap often present.

---

[11] *Tetraceros* (India). Anterior pair of horns very small, especially in young animals. Sometimes not developed at all. Evidence is available that this characteristic is geographically localized in part of the range of the species.

[12] Sometimes the horns are coiled along their axis so tightly as to appear almost straight.

Coat usually in the form of relatively short and closely adhering hair; more rarely, hair greatly elongated in some parts of the body, or coat greatly reduced. Coloration usually uniform and dark or of different shades of yellow. In some species white stripes or bands occur in the anterior part of the head, spots on the cheeks, and longitudinal or transverse stripes on the trunk and legs. Distinct sex-related color dimorphism exceptional. Teats four.

The subfamily includes species of varied general appearance. Some members represent typical, fairly heavy cattle (cattle, buffalo, wisent, and eland); some are lighter in build and intermediate between cattle and antelope (kudu, oryx, and nilgai); one species (four-horned antelope, *Tetraceros*) is similar to the small lightly built gazelle.

These are inhabitants of tropical forests and forests of the temperate belt and forest-steppes, frequently of steppes; exceptionally they inhabit mountains (high altitudes) or are specialized for life in swamps. They live in small groups (sometimes in families) but often singly; they do not form large herds or groups.*

The range of the subfamily is extensive and hence divided into four independent parts. Bovinae are found in North America, where they occupy the central part of the mainland between 26 to 27° and 65° N lat. (reconstructed geographic range); in Asia they inhabit Tibet, India, the Indochinese Peninsula, Ceylon [Sri Lanka], Sumatra, Java, Kalimantan [Borneo], Sulawesi [Celebes], and Mindoro; and the western part of the Near East (Asia Minor, the Caucasus, Palestine, and Mesopotamia); in Africa they are found in North Africa from the Egyptian zone of the United Arab Republic to Mauritania (aurochs, *Bos primigenius,* extinct in the historic past), and south of the Sahara; they occur throughout Europe except in the northeastern part (reconstructed range). From a purely geographic viewpoint the subfamily should evidently be considered Eurasian-African but mostly Eurasian. Domesticated forms which have turned wild are dispersed somewhat more widely in southwest Asia than described above. Domesticated members of the subfamily are distributed throughout the world.

The subfamily adopted in the present treatise (according to

---

*Not true of some species—Sci Ed.

Simpson, 1945) combines a few groups which former (sometimes even contemporary) researchers considered independent subfamilies, such as Bovinae, Strepsicerotinae (Tragelaphinae), and Boselaphinae. It includes typical cattle (Asiatic and African buffalo, wisent, banteng, yak, gaur, and others) and some groups of antelope, i.e., African kudu (*Strepsiceros**), eland (*Taurotragus*), Asian nilgai (*Boselaphus*), and four-horned antelope (*Tetraceros*).

373 Bovinae in the modern interpretation constitute a less natural group than in the older interpretation when they included only cattle proper. The external features of the various members often appear dissimilar or highly identical, which can be explained as due to their great external diversity or parallelism. Some well-known superficial features still persist in the taxonomy of cavicorns and are important. The inclusion of the above groups of "antelopes" is more natural since they are closer to cattle and have little in common with other "antelopes."

There is no doubt that firstly cattle, secondly kudu and eland, and thirdly nilgai and four-horned antelope constitute three natural groups, morphologically as well as phylogenetically. However, their separation is evidently limited to the subfamily level; they may be considered independent in origin even within this category (as tribes Bovini, Strepsicerotini, and Boselaphini).[13] Cattle proper (Bovini) are more specialized and occupy a somewhat "peripheral" position in the family.

Views on groups phylogenetically closest to Bovinae vary. Evidently the closest is the African subfamily Cephalophinae ("duiker," 2 or 3 genera, 19 species).

Bovinae are known from the Lower Miocene (the earliest—*Protragoceros*) but were evidently very few at that time. In the Upper Miocene they increased and became abundant during the Pliocene. In the Miocene period Bovinae are known only from Europe and Asia; in Africa they are known from the Lower Pliocene; they appeared in America only during the Pliocene. Primitive Pliocene Bovinae were similar in form to large antelopes (nilgai and eland), usually with lyrate or spiraled horns directed backward. The earliest forms (including *Protragoceros*) belong to Boselaphini (nilgai) and Strepsicerotini (kudu and eland). True cattle (Bovini), originating from them, appear only in the Middle Pliocene of Asia in their typical form. The quite slender "antelope-like" cattle (*Leptobos*) appeared in the Upper Pliocene of Eurasia. Thus, Strepsicerotini and Boselaphini should be regarded as the most primitive members not only of Bovini but of Bovidae as a whole. The place of origin of the subfamily is evidently Eurasia.

---

*According to modern taxonomists genus *Strepsiceros* has been relegated to a subgenus and included under genus *Tragelaphus*—General Editor.

[13] The merger of Boselaphini with Bovini into a common tribe (Sokolov, 1949 and 1953) as yet lacks adequate substantiation.

The subfamily includes a large number of fossil genera (see below) representing Recent groups (tribes) of Bovinae. Boselaphini are well represented among fossil forms (16 genera in Asia, partly in Europe). They include present-day African "screw-horned antelopes" (Strepsicerotini) as well as present-day cattle and buffaloes (Bovini).

Different researchers include within the subfamily a different number of genera; moreover, the tendency to subdivide, especially cattle, still prevails. At present the subfamily includes (Simpson, 1945) 40 genera—30 fossil and 10 extant (about 18.5% of present-day Bovidae)—which are usually divided into three (or two) tribes. Tribe Strepsicerotini includes two genera—kudu (*Strepsiceros* including *Tragelaphus* and *Limnotragus*) with five species (*strepsiceros, imberbis, spekei, angasi,* and *scriptus*) and eland (*Taurotragus* including *Boocerus*) with two species (*euryceros* and *oryx*). Tribe Boselaphini includes two genera—nilgai (*Boselaphus*) with one species (*tragocamelus*) and the four-horned antelope (*Tetraceros*), also with one species (*quadricornis*). Tribe Bovini, typical cattle, includes six genera—Asiatic buffalo (*Bubalus*) with one species (*arnee-bubalus*); (the Philippine buffalo *B. mindorensis* is often regarded as a distinct species rather than a subspecies); dwarf buffalo of Celebes (*Anoa*) with one species (*depressicornis*); true cattle (*Bos*) with two species (aurochs, *primigenius* and yak, *mutus*); cattle with
374 broad foreheads (*Bibos*) with three species (gaur, *gaurus*; banteng, *javanicus-banteng*; and Indo-Chinese gray cattle or kouprey, *sauveli*)[14]; African buffalo (*Syncerus*) with one species (*caffer;* sometimes the dwarf buffalo, form *nanus* is regarded not as a subspecies but as a separate species); and bison (*Bison*) with two species (European wisent, *bonasus* and American bison, *americanus**).[15] Thus the

---

[14] Gayal (*Bibos frontalis*) is not an independent species but only a domesticated form of gaur which, at some places, has turned feral.

Gray cattle were discovered only in the 1930's (described in 1937) and very little is known about them to date. One view holds that they do not constitute an independent species but are only a hybrid of banteng with gayal, gaur, or domestic cattle.

This species has been isolated in a separate genus (*Novibos*) without adequate justification. Here, it is included in genus *Bibos*, based on the findings of Sokolov (1953). Probably, it would be more correct to place it in genus *Bos*.

**B. americanus=B. bison*—General Editor.

[15] Sometimes yak (*Poëphagus*) and, as stated before, gray cattle or kouprey (*Novibos*) are isolated in separate genera. Contrarily, genera *Bos, Poëphagus, Bibos,* and

subfamily consists of 19 species, or 21 if *B. mindorensis* and *S. nanus* are treated as independent species. The subfamily comprises therefore about 14% of the species of the family.

Of the ten present-day genera, three are exclusively African (*Strepsiceros,** *Taurotragus,* and *Syncerus*), five exclusively Asian (*Boselaphus, Tetraceros, Bibos, Bubalus,* and *Anoa*), one Eurasian (*Bos*; in the past also North Africa), and one Eurasian-American (*Bison*). The corresponding number of species are seven, six, three, and two.

The economic importance of the group, apart from what has already been stated (see description of the family) is great primarily because five species, of which four are also encountered in a wild state, represent extremely important domestic animals (cattle, yak, banteng, buffalo, and gayal).

Wild species of the subfamily are absent in the USSR today. Aurochs (*Bos primigenius*) and yak (*Bos mutus*), evidently present in a wild state in the USSR earlier, are altogether extinct. Although a few wisent have survived, they are not found in a wild state and represent an animal strictly protected either in special nurseries or in wild animal parks. Domesticated species in the USSR, apart from descendants of aurochs, i.e., large-horned cattle ("*Bos taurus*"), include yak ("*Bos grunniens*") and Indian buffalo ("*Bubalus bubalis*"). The latter did not survive in the USSR in a wild state.

Taking into account aurochs, yak, and wisent, Russian fauna includes two genera (20% of present-day genera) and three species (about 16% of present-day species) of Bovidae, constituting 0.9% of all species of Russian fauna. (V.H.)

Genus Aurochs, or Typical Cattle

Genus *Bos* Linnaeus, 1758 (Cattle)

1758. *Bos*. Linnaeus. *Syst. Naturae,* 10th ed., p. 71, *Bos taurus* Linn. (domestic cattle).
1814. *Taurus*. Rafinesque. *Princip. Somiol.,* p. 30. Substitute for *Bos* Linn.
1827. *Urus*. H. Smith. Griffith's *Cuvier Anim. Kingd.,* vol. 4, p. 417.

Novibos are often united in genus *Bos,* and *Bubalus* and *Syncerus* in genus *Bubalus.* Such a scheme would be more natural in many respects. Sometimes *Bison, Anoa, Bubalus,* and *Syncerus* are included in genus *Bos.* It might be more correct to take advantage of a broad concept of the genus and divide it into subgenera rather than establish separate genera.

**Strepsiceros=Tragelaphus*—General Editor.

(V.H.) *Urus scoticus* Smith (Scottish park cattle).
1843. *Poëphagus.* Gray. *List Mamm. Brit. Mus.*, p. 153. (V.H.)

Bos are large animals of the tribe Bovini, massive and heavy in build, standing on relatively short legs. Body proportionate but anterior part of trunk not particularly massive; shoulder region and withers low and back straight or withers slightly raised; back almost straight or slightly inclined. Head heavy and set low.

375 Thoracic vertebrae 13 or 14. Spinal process of seventh cervical vertebra short. Spinal processes of posterior vertebrae fairly short, their length gradually diminishing toward the rear, or very short and diminish rapidly in length toward the loin.

Skull relatively elongated and narrow (basal length of skull roughly twice distance between orbits). Frontals not enlarged, but flat; their posterior margin forms between the horns a very prominent or smoothened crest (ridge); parietals do not extend into facial part of skull. Pneumatization of skull very pronounced. No preorbital depression on lacrimal. Ethmoid pit absent or very small (slit). Orbits project sideways relatively little; nasals elongated and not broadened in the middle.

Horns set high (above the skull); bases wide-set on lateral side of skull. Horns circular in cross section, smooth (with indistinct wrinkles at base), and relatively long; initially directed sideways, then upward and forward, sometimes upward and slightly inward; either black or light-colored but black at tips. Females horned.

Glands absent on face, flanks, and limbs. Tail fairly long, reaching calcaneal joint, or even further; completely covered with long, shaggy hair or with short hair with a tassel of long hair only at the end. Dewlap present.

Entire body covered with short hair of uniform length or hair on underside (elbow region, abdomen, down the sides, and thigh) highly elongated. Beard absent. Color, uniform black; legs same color as trunk. Female slightly smaller and lighter than male, with somewhat weaker horns. In one species (aurochs) females and young differ markedly from adults. Teats four.

Bos inhabit the southern parts of the forest zone, forest-steppe, and steppe, and also high-altitude regions. They do not form large herds and live mainly singly or in small family groups. They produce a single calf in any gestation period.

Presently these animals are found wild only in Tibet; in the past were evidently known in the mountains of Mongolia and southern Siberia (one species) and in western and central Europe, in the western European part of the USSR, in the Caucasus, and in Central Asia including Mesopotamia, and North Africa.

Several species of the genus were widely dispersed in the Pleistocene in Europe and Asia; one evidently even reached Alaska. The earliest member of the genus has been traced to the Upper Pliocene (India, North Africa, and the Caucasus). The ancestral stock which gave rise to genus *Bos* was evidently the mid-Pliocene, Central Asian *Urmiabos* (Sokolov, 1953).

In the narrow sense adopted here (see characteristics of the subfamily), genus *Bos* consists of only two species—the present-day yak (*Bos mutus* Przevalski, 1883) and the already extinct aurochs (*Bos primigenius* Bojanus, 1827). The differences between these two forms are sharp and they evidently existed independently for a long time (from Middle Pliocene). Placing them in different subgenera appears justifiable—aurochs in subgenus *Bos* Linnaeus, 1758 and yak in *Poëphagus* Gray, 1843. Morphologically, especially in terms of craniology, they are nonetheless closely related. Yak combine the features of genus *Bos* and genus *Bison* and occupy a somewhat intermediate position between them. This justifies the merger of genera *Bison* and *Bos* suggested by many taxonomists.

Aurochs as a wild species became extinct in the seventeenth century but their descendants, large horned cattle ("*Bos taurus*"), are now dispersed throughout the world as the most important domestic animal of man. Small numbers of yak still survive in a wild state in Tibet and also play an important role throughout Central Asia as domestic animals.

In the USSR members of genus *Bos* are absent in a wild state but there is no doubt that aurochs and probably yak did live in Russia at one time. They represent 10.5% of the species of the subfamily and 0.6% of species of the USSR fauna. (V.H.)

376 8. AUROCHS, PRIMITIVE CATTLE[16]

Bos (Bos) primigenius **Bojanus, 1827**

1827. *Bos primigenius.* Bojanus. *Nova Acta Acad. Leop.-Casol.*, vol. 13, no. 2, p. 422.[17]

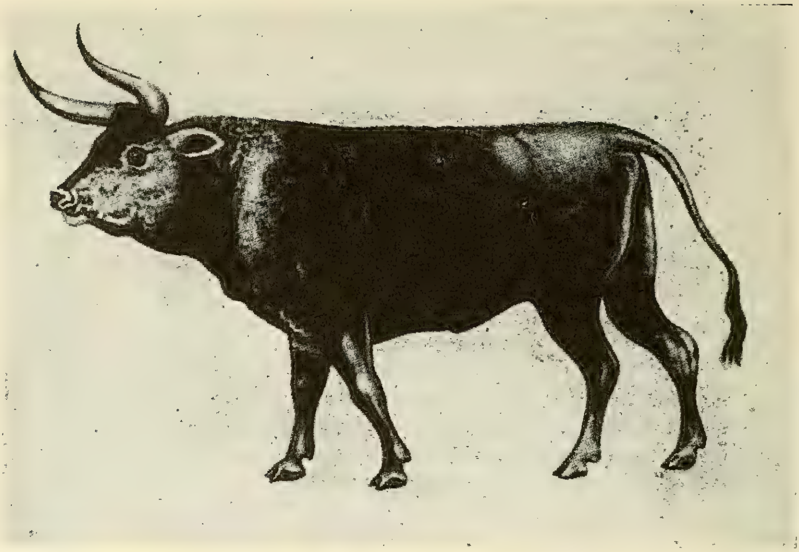
---

[16] The first common name (used in "bylinas" [Russian epics]) is more widely used, and is in scientific literature; the second "primitive bull," is purely bookish and artificial (translated from Latin), and is rarely employed.

The root of word "tur" [=aurochs] lies in the Latin word "urus". This term was used to denote aurochs even by Julius Caesar while describing the Hercynian forests in his "Notes on the Gaulic Wars".*

*Verification of the etymology of "tur" not possible; see earlier footnote regarding confusion of "tur" and "aurochs" by Heptner—General Editor.

[17] Although the Latin name of the aurochs with the suffix *primigenius* and a



376 Fig. 115. Augsburg drawing of tur, *Bos primigenius* Boj. Original, circa 1525 (from Lengercken, 1955).

The external features of tur, which became totally extinct as a wild animal more than three centuries ago, and its craniological and skeletal characteristics are well known. Folklore, and descriptions by travelers (Gerbershtein, 1557), drawings in ancient texts (Tesner, 1563), especially the "Augsburg drawing," various historical evidences, and innumerable drawings of tur on utensils and other archaeological objects are available. The number of remarkable wall drawings made by prehistoric man in caves of Spain and France is indeed large. Paleontological material is also vast.[18]

reference to Bojanus is widely used, it is not above reproach from a nomenclatural point of view (Harper, 1945).

The suffix *primigenius* is used here as a specific and not as a subspecific term (in relation to *Bos taurus*) as is commonly done. In my opinion domestic forms cannot and should not lend their names to wild ancestors since the relations between domestic forms and original wild ones are not the same as the relation between subspecies (geographic races) of the same wild species. The trinomial nomenclature, however, is designed to reflect this category of systematic and genetic relations. In order to display the relations between wild and domestic forms, some other type of nomenclature ought to be used, preferably devoid of the Latin nomenclature used to designate wild fauna (V.H.).

[18] Literature on aurochs including zoological, breeding, historical, and archaeological, is very extensive. Here the subject has been dealt with very briefly in very general terms (Belyaev, 1865; V.I. Gromova, 1930 and 1931; Hilzheimer, 1930; V.I. Gromov, 1948; Harper, 1945; Hainard, 1949; Lengercken, 1953 and 1955; Vereshchagin, 1956; and others).

The bulls were enormous, considerably larger than present-day
377 domesticated bulls. Their height at the shoulder was 170 to 180 cm and weight 600 to 800 kg. According to some evidence height at the withers even reached 200 cm. These figures, however, pertain to a very early period; in the last century of their existence aurochs were smaller and their height did not exceed 150 cm. Cows were significantly smaller than bulls. The difference between the two, judging from some data, was greater than the corresponding difference in present-day domesticated animals.

In general appearance the aurochs was an animal of relatively light build, with anterior part of body moderately massive, and legs fairly long. It was much lighter and more slender than our domestic cattle. Withers were not very high, back straight, only rising slightly toward the withers, and the croup straight. Head was proportionate, set fairly high, forehead quite narrow, with a straight profile very similar to the head of domestic cattle. Horns large, very sharp, and light-colored with dark tips. They arose from the skull initially sideways, later upward, forward, and slightly inward, with the terminal part directed up. When the head was inclined, the sharp tips of the horn pointed forward. Ears not large and tip of muzzle bare. Neck massive with a small dewlap. Tail not long, its tip extending only slightly below the hock. Cows, in general appearance, particularly during the growth of horns, did not differ significantly from bulls, but were much lighter in build. Anterior part of trunk was less massive and the head lighter.

The summer hair was evidently short and close, but somewhat longer than that of domesticated cattle. Almost the whole of the tail was covered with short hair, with a tassel of long hair only at the end. On the forehead, between the horns, the hair was long and curly. The hair on the withers was also, evidently, slightly elongated. The winter hair was longer and quite shaggy, longer than that of domesticated cattle.

Aurochs exhibited sharp color differences between the sexes. Bulls were uniform by black or black with a brownish tinge. The tip of the muzzle (chin and hair along the edge of the bare portion) was light-colored; a narrow, light-colored (almost white) band, very characteristic of aurochs, extended along the back. Evidently the adbomen and the inside surface of the legs were lighter in color than the trunk. Cows were a rusty-brown (bay-colored) and evidently also had a narrow light-colored band on the back. The winter color of cows was darker. The first coat of hair of calves was bright bay-colored, similar to that of cows or even brighter.

Aurochs were characterized by a certain amount of individual

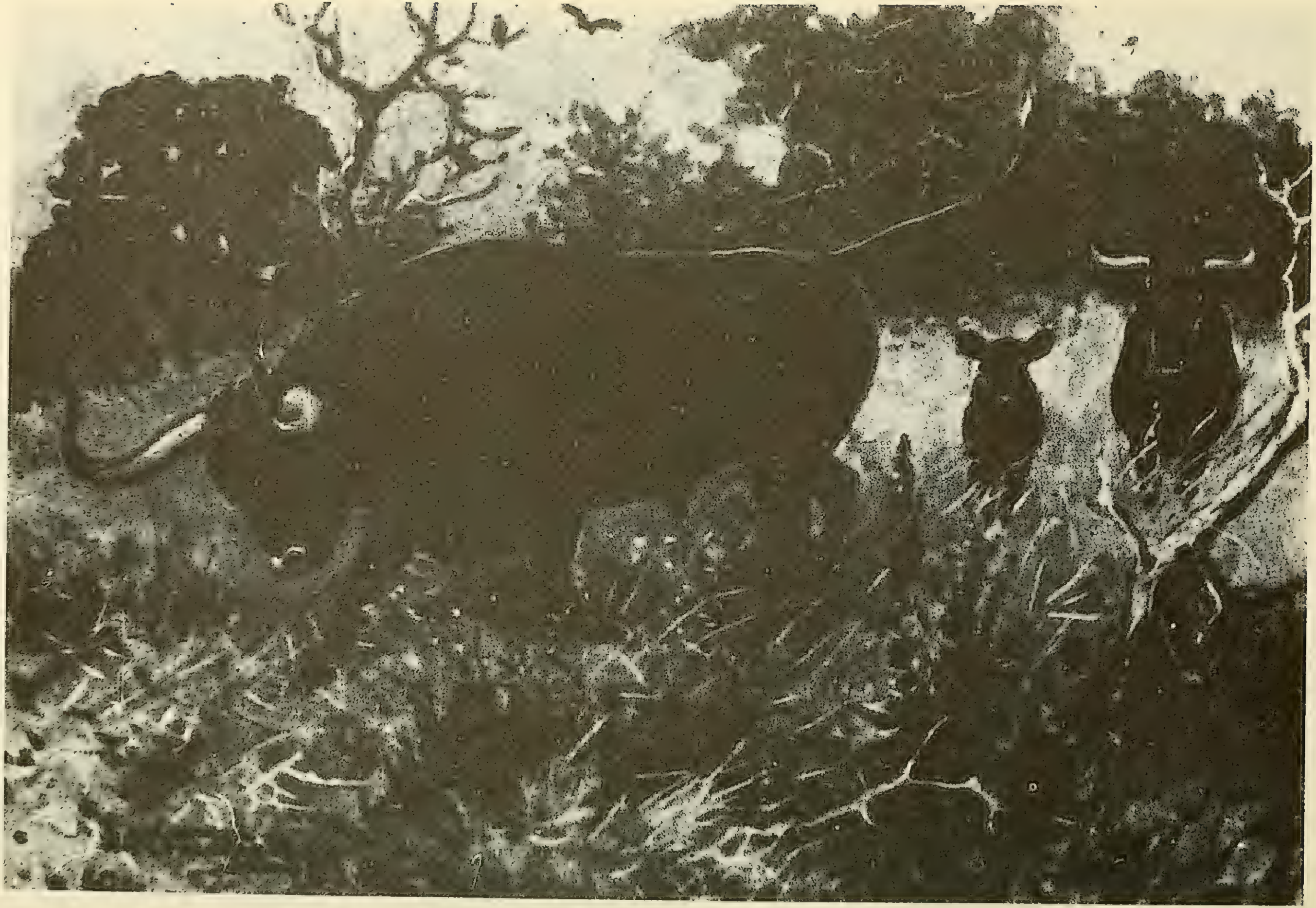


Plate 3. Aurochs (primitive bull), *Bos (Bos) primigenius* Boj. Sketch by A.N. Komarov.

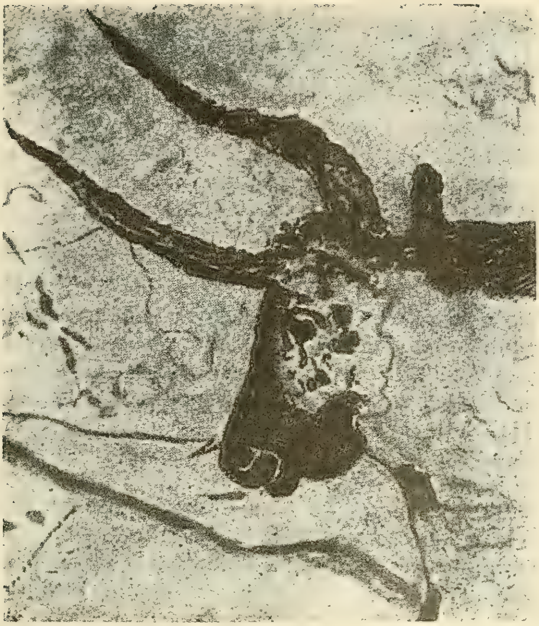


Fig. 116. Sketch of aurochs (in part) made by prehistoric human on the wall of Lascaux cave in southern France, discovered in 1940. Original about 5.5 m long and black in color. Sketch usually dated between Aurignacian and Magdalenian, around 25,000 years B.C. According to some computations it is Aurignacian and circa 50,000 years old; according to others it is Magdalenian or 1,500 [*sic;* 15,000] to 10,000 B.C. (from Lengercken, 1955).

variability. As far as can be judged from the drawings of prehistoric
378 man and from available paleontological material, variability was manifested in general build and in size and shape of horns. The latter invariably, at least in bulls, had forward-directed tips but the shape of their bend, at the base, evidently varied. They were not always bent in exactly the same manner as described above or depicted in drawings. Apparently the horns of cows were more often irregular in shape. The intensity of color also varied and sometimes (very rarely) cows exhibited the dark color characteristic of bulls.

The probability of free hybridization of aurochs with domesticated cattle was high due to the existence of wild aurochs during the last millenium, which may have enhanced variability.[19]

In an animal with an extensive distribution (from the Scandinavian Peninsula to North Africa and Mesopotamia), living under extremely diverse natural conditions, geographic variability would inevitably be prominent. But very little is known about this aspect. There were evidently differences in size as well as in color. Aurochs of North Africa were a bright rusty color. In Russian epics aurochs figures frequently and references to "bay-colored types" exist. It is possible that aurochs of the Dnieper region were so colored, but it is more probable that their coloration was that described above.

---

[19] Among the last aurochs held in captivity, there were definitely some hybrids produced with domesticated cattle, some of which were even piebald.

The systematic position and the affinities of this form, i.e., *Bos primigenius* proper, which became extinct before our century, as well as the boundaries of its distribution in the remote past, are not yet fully known. From the Pleistocene, even from the beginning of the Pliocene as well as from the uppermost Pliocene, many species and subspecies of the genus *Bos* have been described. Some researchers recognize five or six species of this genus in the USSR. It would be more correct to accept (V.I. Gromova, 1931) only two, i.e., glacial (*Bos trochoceros*) and postglacial, Recent (*Bos primigenius*), a descendant of the former. The other species are only geographic or chronological races or individual variations. This concept is very convincing.

Aurochs were widely dispersed. Fossil remains and other evidence (drawings) about their distribution pertain to glacial and postglacial periods in North Africa from Egypt to Mauritania, throughout Europe up to 60° N lat., from the southern Urals and Trans-Urals and southwestern Siberia (from Ishim, Altai, and central Altai plains), around Krasnoyarsk, from Trans-Baikal, Manchuria, China from 40° to 50° N lat. and in the east up to the Pacific Ocean, and from Turkmenia (Annau, around Ashkhabad), the Caucasus, Crimea, Asia Minor, Palestine, Mesopotamia, and certain other adjacent regions.

Some of this information pertains to *Bos trochoceros,* and part undoubtedly to aurochs, but from a very remote past. Hence it is extremely difficult to identify those places in the above distribution where aurochs lived in the historic past, let alone the last millenium. Archaeological, folklore, and historic material permit one to assume that in the historic past tur were present in North Africa (Egypt, northwest Africa, and Mauritania); throughout southern, central, and western Europe, including England (they were evidently absent in Ireland), in the north up to southern Sweden[20]; and in the Balkans, Asia Minor, Syria, Mesopotamia, and probably southern Turkmenia.[21]

[20] Skane, Smaland, and Oland Islands and in the north to Ostergotland, i.e., to the northern extremity of Lake Vettern (Ekman, 1922).

[21] Turkmenia is dubious since positive information about the distribution of

In the European part of the USSR aurochs lived in the Baltic republics, Lithuania, Belorussia, the Dnieper basin (in any case,
379 around Chernigov and Kiev), and probably in the Don basin, at least in the upper part of it. In the north they occurred in the east up to the Novgorod region and the southern bank of Lake Ladoga (the northernmost point of distribution of the species). It is possible that the animals lived or intruded into the districts of Ryazan', Tula, Kaluga, Moscow, Smolensk, Kalininsk, Yaroslav, and Novgorod.[22] Midway in the first millenium of our epoch, the aurochs was widely dispersed in the steppes of the Ukraine and even up to the Caucasus; excellent drawings of the animal are known from Chertomlyts and Maikop burial mounds (Vereshchagin, 1956).

The range of aurochs in Russia apparently formed an irregular triangle with the western boundary of Russia as its base, commencing in the north from Lake Ladoga and the Gulf of Finland. The apex of the triangle covered the Don basin and extended in the form of a projection as far as the Caucasus. The northeastern boundary probably bypassed Moscow to the south. The distribution of this animal, surviving mainly on grass, was probably hindered in the northeast by abundant snow and its annual duration. Aurochs could hardly cross the line where the thickness of snow exceeded 50 cm.

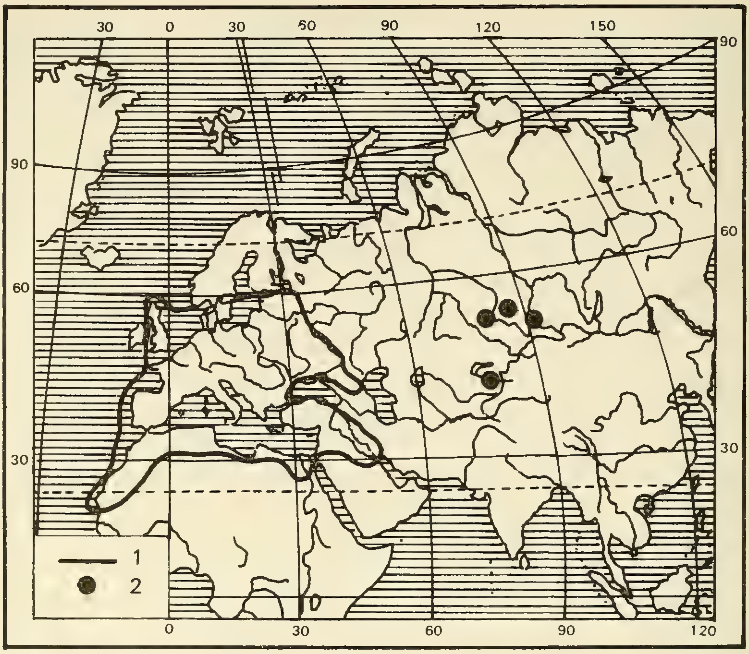
Apparently in prehistoric times aurochs also lived in western Siberia and Kazakhstan, but information is so scarce one cannot depict the range of the animal there, nor assess the relationship of these occurrences with those in Europe. Drawings of aurochs, dating a few thousand years back, exist in the Minusinsk depression. Later drawings have been discovered on rocks in the Chulak mountains in the middle reaches of the Ili (Rygdylon, 1955; Marikovskii, 1953). Information is available about the occurrence of aurochs in the Kamensk okrug of the Kulunda steppe in the sixteenth or seventeenth centuries and around Kuznets in the eighteenth century (Vereshchagin, 1956).

380 Very little information is available about the biology of aurochs. In Europe, at least in historic times, it was confined to forests, even to dense, damp, and swampy forests. However, it undoubtedly lived in sparse forests in some parts of its range, or even in much of it, or

---

aurochs in Iran is not available. Ancient drawings of bulls (extremely stylized) from Iran are probably based not on an acquaintance with the animal but rather represent motifs in Assyrian sculptures. Later the animal's shape was greatly distorted and took on the look of abstract symbolism.

[22] The assumed distribution in the central and eastern parts of Vologod district along the Dama, and in the Trans-Urals (along the Tura River) is not adequately supported.



379 Fig. 117. Suggested specific geographic range of aurochs, (*Bos primigenius* Boj.) in the historic past. Dots indicate individual occurrences in Kazakhstan and western Siberia mentioned in literature (explanation in text). V.G. Heptner.

at places where forests were interspersed with meadows, in forest-steppes, or even in open steppe expanses with poor forest vegetation (bottomland forests), or possibly regions devoid of such vegetation (Africa). In Europe, during their last century, they preferred open meadow pastures in summer and migrated in winter to forests, feeding there partly on twigs.

It is highly probable that the dense forest massifs in which the last of the Lithuanian and Polish aurochs actually lived represented their last refuge (true also of wisent [European bison]) from persecution by man. At places (Pyrenees) aurochs lived in mountains up to the level of alpine meadows.

Aurochs lived in small groups. According to some evidence they formed herds mainly in winter, living singly by and large in summer. In addition to grass and shoots of trees and shrubs, acorns were an important dietary item in autumn. The animals mated in September and calved in spring.

Aurochs possessed a wild and vicious temper, were not afraid of man, and were highly aggressive. In Russian folklore and literature they symbolize not only power but also bravery ("for he was as valiant as an aurochs", "wild bull' Vsevolodovich"). Hunting such powerful and mobile animals (in Russian epics aurochs are depicted as very agile and rather fleet-footed) was very dangerous and looked upon as an act of valor. An outstanding hunter of bygone days, Vladimir Monomak, wrote that "two aurochs threw me down from a horse". The small number of aurochs remains in ancient human settlements compared with abundant wisent remains has been explained by some researchers as due to the fact that aurochs were extremely dangerous, and too difficult for Paleolithic and even Neolithic man to catch. Adult bulls often fought among themselves and evidently also with wisent. They had no enemies worth the name and were not afraid of wolves; only calves and juveniles feared wolves.

In the extensive territory under description aurochs became extinct, partly because driven away by cattle breeders at different periods long ago. In Egypt wild aurochs had disappeared even before 2400 B.C. They survived in Mesopotamia evidently for a longer period and thrived during the days of the Babylonian empire; they are not mentioned in the much later Assyrian empire (around 600 B.C.). In central Europe aurochs were evident even in the Middle Ages and still surviving at places, for example along the Rhine, up to 1300 A.D. In the twelfth century (at least at the beginning of it) wild aurochs were known along the Dnieper, especially in the Chernigov lands. Prince Vladimir Vsevolodivich (Monomakh) hunted them during the days of the Chernigov empire.

By 1400 A.D. aurochs had disappeared in central and western Europe but were still found in the Kaliningrad district and later were preserved in Poland (particularly in Mazovieeki) and to a certain extent in Lithuania for a long time. During the last few centuries of their existence, before the date of the death of the last aurochs (1627), the animals lived under the protection of special legislation and later were preserved in royal hunting grounds. They were protected and haystacks placed on the grounds for them during winter. The demise of aurochs in central Europe coincided chronologically and was largely associated with the "era of clear-cutting" from 800 to 1100 A.D. (in the eleventh century, they were still common in the royal hunting grounds at Vogezakh). Their preservation in Poland and Lithuania was evidently the result of the inaccessibility of their habitation and sparsely populated forest expanses.

Aurochs are the ancestors of European cattle. In a few of the more primitive varieties of cattle some aurochs characteristics are still distinct. Such forms include Scottish and English park cattle, Hungarian steppe cattle, gray Ukrainian cattle and others, espe-

381 cially cattle used in bull-fights in Spain and southern France, particularly semiwild Camargue cattle (Rhone estuary).

The preservation of the more typical characteristics of aurochs in cattle used in bullfights is explained primarily by selective breeding of the animal as demanded by local traditions over a very long period. This is particularly true of the shape of the horns and black coloration. However, cattle used in bullfights do not represent a homogeneous form; there are among them distinct "lines" associated with various ranches ("ganaderia") breeding animals specifically for "corridas" (bullfights). In some lineages aurochs features are more distinct than in others.[23]

The domestication of aurochs occurred around 4,000 years ago (2000 B.C.) in southeastern Europe (in Greece). From there, domesticated forms spread west and northwest into the Baltic Sea basin and became highly diversified.

Some attempts were made in the last decade to "restore" aurochs, i.e., to produce an animal with the appearance of aurochs. Of particular interest in this context are the efforts made in Berlin Zoological Garden (L. Heck) and in Munich (H. Heck). By careful selection of material from several primitive domesticated races, primarily Spanish fighting bulls, and through selection, it has been possible to produce extremely interesting results in a surprisingly short period. The Berlin animals, in which a greater resemblance to aurochs was produced, died during World War II. In Munich, however, the animals produced in the 1950's were essentially quite similar to tur but somewhat heavier. They not only have the typical overall black coloration, characteristic horns, and certain other features of aurochs, but even the light-colored band along the back. It has been possible to restore even the bay color of the cows and the juveniles, i.e., to obtain sex- and age-related dimorphism so characteristic of
382 aurochs. This is of particular interest because these dimorphisms were absent not only in the animals chosen for the experiment, but also in other present-day breeds of domesticated cattle.

The "restored" aurochs is usually considered a special form of domesticated cattle in which a purely phenotypical copy of tur has been induced.[24] The manifestation in them of age- and sex-related

---

[23] Camargue cattle are particularly interesting in this respect. Although quite small, they have preserved the general appearance of tur evidently to a far greater extent than others. Their extreme lightness and mobility, and their ability to run and jump are noteworthy. In these features they surpass not only other domesticated species but also Spanish fighting bulls (extremely interesting photographs have been presented by Drechsler, 1958).

[24] A special resolution with regard to this subject has been adopted by the Conference of Directors of German Zoological Gardens.

381 Fig. 118. "Restored aurochs" of Munich Zoological Garden. Photograph by Heinz Heck.

dimorphisms characteristic of genuine aurochs renders the recreated animals as something different from domesticated cattle. (V.H.)

9. YAK

Bos (Poëphagus) mutus **Przevalski, 1883**

1776. *Bos grunniens.* Linnaeus. *Syst. Naturae,* 12th ed., vol. 1, p. 99. "Northern Asia." Description of domesticated animal.

1811. *Bos poëphagus.* Pallas. *Zoographia Rosso-Asiatica,* vol. 1, p. 248, tab. 22. Renaming of *Bos grunniens* Linn.

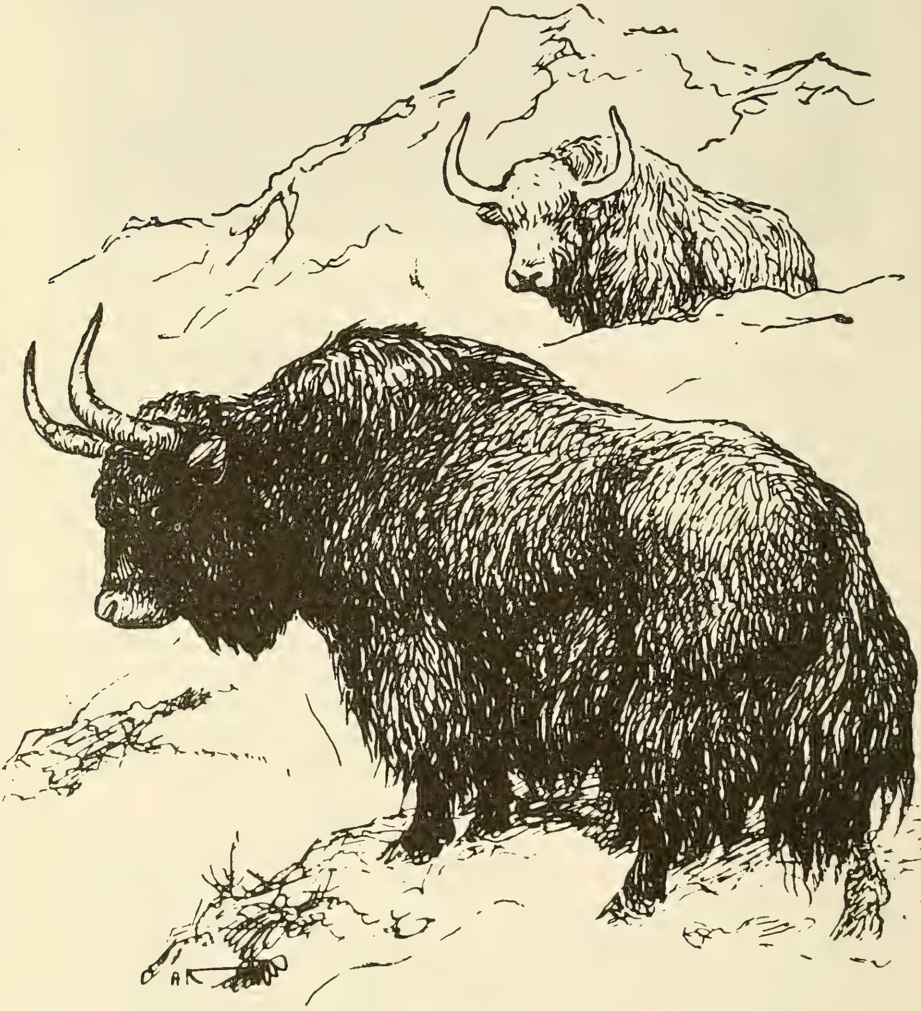
1883. *Poëphagus mutus.* Przewalski. *Third Journey into Central Asia,* p. 191; table on p. 120. Alpine zone of western part of Nan Shan (roughly 39°20′ N lat. and 95° E long.) between Anembar-Ula in the west and Humboldt range in the east.[25] (V.H.)

Bull large with a massive, fairly long trunk, relatively short legs, and a large, heavy head. Withers elevated and form gentle slope backward. Horns large, initially set straight and sideways, turning later upward and slightly forward, with the tips turned upward and slightly backward and inward. When the head is inclined for an attack, the tips point frontward. Much of the body coat is uniform, dense, and relatively short. On the anterior extremities, chest, down the sides, along the abdomen, and on the hind legs, at the level of the knee joints, very long shaggy hair forms splendid tresses like a "skirt," which imparts to the animal an entirely distinctive appearance. Tail covered from the base, as in horses, with long hair de-

---

[25] Since the first two names refer to domesticated animals, the name given by Przewalski is used here (see footnote no. 17 of this chapter).

The type locality was not indicated by Przewalski but is given here based on the more accurate data of Harper (1940).



383 Fig. 119. Yak, *Poëphagus mutus* Przev. Sketch by A.N. Komarov.

scending almost up to the hock, i.e., almost as far as the hair on the sides and hind legs. Hair on tail very dense and forms a magnificent whisk or thick tassel, much shorter but thicker than in horses.

Color of animal pure black, acquiring a brownish tinge on the back and in the upper parts of the sides in old males. Muzzle gray. In younger animals a narrow and indistinct gray band occurs along the middle of the back.

Thoracic vertebrae 14 and spinal processes of the first few highly elongated. Body length of adult bull about 330 cm, tail length about 90 cm, and height at shoulders about 180 cm. Horns large, black, and 96 cm long. Cows much smaller and lighter with weaker horns. Their height at the withers about 145 cm.

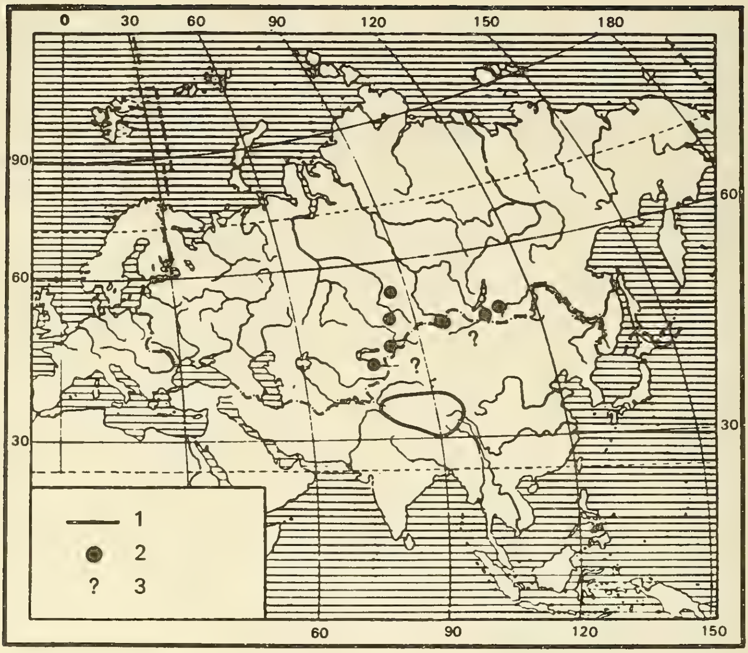
From time immemorial until recently it was thought that yak lived in a wild state, and continued to do so, only in Tibet. A recent study of some paleontological and archaeological material and historic evidence has revealed that wild yak also lived in the Soviet Union, not only in the Holocene but also during historic times and even during the thirteenth to the eighteenth centuries A.D. During this period wild yak probably lived in the northwest as far as to Tuva and Dzhungaria, perhaps even to the Kuznets Alatau. The oldest evidence pertains to the early fourteenth century as given by
384 Rashid-Ad-Din (1952). While describing the distribution of a tribe of Uryankats (natives of Tuva), Rashid-Ad-Din states that in winter many animals, including mountain bulls, were killed in their country in large numbers on deep snow. It is also reported that Uryankats caught juvenile mountain bulls and cows, and domesticated them. What Rashid-Ad-Din calls "mountain bulls" were probably yaks.

A few centuries later, in 1720, Bel' traveled through Siberia. According to him (1776) there were some animals around Kuznets which the local inhabitants called "bubul". The most distinguishing feature of these bulls was their tail—similar to that of horses.[26]

A few years after the travels of Bel', in 1739, an order was sent to Siberia commanding that wild animals should be caught and turned over to the royal palace. Among the animals were "bulls and cows with tails like those of horses." Soon after this V.N. Tatishchev wrote his *Vvedenie k gistoricheskomu i geograficheskomu opisaniyu Velikorossiiskoi imperii* [Introduction to an Historic and Geo-

---

[26] In the forest around Kuznets, according to Bel', . . . "there is yet another type of bull (apart from wisent, V.H.) called bubul by the Tatars. It is less stout than the wisent but the two are quite comparable in size. It is high at the shoulders and has a tail with long hair extending right from the base up to its tip like that of a horse" (cited from Vereshchagin, 1956; V.H.).



384 Fig.120. Distribution of Yak, *Poëphagus mutus* Przev.

1—reconstructed and present-day geographic range in Tibet; 2—points of distribution in the past in the USSR for which references are available about the occurrence of yak from the Upper Pleistocene and Paleolithic and up to the eighteenth century (explanation in text). Question marks indicate territories (Mongolia and western China) in which the occurrence of yak in the past was likely but no supportive information is available. V.G. Heptner.

graphic Account of the Great Russian Empire] (1950) in which it was stated that quite a few bulls and cows with tails like those of horses were sighted "around Altai mountains and in Dauria," and that one cow had been sent to the royal palace in 1735[27] (S.V. Kirikov).

Some rock drawings in the Chulak mountains (midcourse of the Ili; Marikovskii, 1953) also depict yak (Vereshchagin, 1956). N.K. Vereshchagin (1954), in substantiating the occurrence of yak in the Pleistocene in Trans-Baikal (around Chikoya and in the Chernyshev
385 region of Chita district), affirms that the wild yak is a descendant of the Pleistocene Trans-Baikal *Poëphagus baicalensis* N. Ver., and disappeared in Mongolia and Trans-Baikal under the influence of

---

[27] Shipments of "bulls with horse tails" from Siberia to the royal palace in the capital were frequent in the eighteenth century (V.H.).

man in the historic past. According to this author (1956) wild yak were distributed in eastern Kazakhstan at least at the commencement of our era and in the Altai steppes even as late as the eighteenth century.[28] Upper Paleolithic remains of yak are known from Altai (Ust-Kanšk cave).

The above information exhausts all the factual material on the existence of wild yak in the Soviet Union. It includes some inaccuracies along with fairly reliable data. It is quite probable that in the places mentioned above, if wild yak actually existed in them at all, they were animals which had turned feral. This could be the case in the reference given by Rashid-Ad-Din (reference to catching and domestication). Such an assumption is all the more likely for information pertaining to the eighteenth century. There is even justification for assuming that during this period domesticated yak were simply turned over to the capitol. It should be emphasized that all these data pertain to places where domesticated yak were raised for a very long period (right at the time of the report), or to places very nearby. It is also important to note that such a thorough investigator as Pallas did not refer to wild yak of the eighteenth century even though he describes in great detail the domesticated yak. Yak which lived and multiplied in the Moscow menageries ("in vivario mosquense") and which Pallas saw (1811) were domesticated animals. There is no doubt that these animals were those "sent" from Siberia and referred to in various reports.

The fact that until now no precise information has been available about the distribution of genuine wild yak in China outside of Tibet and Mongolia also arouses doubts. It is difficult to conceive that wild yak were preserved in the last century, apart from Tibet, only in Tuva, the Altai, and Kuznets mountains. All this compels one to wait for the results of further archaeological as well as historical studies (Chinese sources, for example), and not include wild yak among Russian fauna just now.

The occurrence of wild yak is limited to Tibet and the area of its distribution has decreased in the last few decades. The population of the animal, which Przewalski saw in thousands, dropped rapidly; if adequate measures are not taken soon, the animals will evidently face extinction. The reason for this lies in their persecution even in Tibet, as a result of the events of the last few decades and the use of modern firearms.

---

[28] Vereshchagin evidently relies on the wording of an order of Queen Anna Ioannovna dated December 29, 1739 to the Siberian governor. This states that "large wild sheep with twisted horns are present around Semi-Palatnaya fort (Semipalatinsk—V.H.) and also wild horses and bulls with horselike tails in some areas close to Kontaishinsk estate . . . " (cited from Vereshchagin, 1956). It appears, however, more probable (with reference to places near Kontaishinsk estate) that this reference pertains not to the steppes but to the montane Altai (V.H.).

Domesticated yak are widespread in Central Asia. In the USSR they are raised in the Pamirs, at some places in the Tien Shan, and in the southern Altai. The domesticated form differs greatly from the wild in its smaller size and in being piebald and hornless. The domesticated form produces hybrids with domestic cattle. (V.H.)

Genus Zubr [=Wisent]

Genus *Bison* H. Smith, 1827

1837. *Bison.* H. Smith. Griffith's *Cuvier Animal Kingdom,* vol. 5, p. 373. *Bos bison* Linn.

1844. *Bonasus.* Wagner. Schreber's *Säugeth., Suppl.,* vol. 4, p. 515. *Bos (Bison) bison* H. Smith=*Bos bonasus* Linn.

Very large species of Bovini (one of the largest in the family[29]), with a massive and heavy build typical of bulls. Trunk with a very 386 powerful thoracic portion and relatively poorly developed hind quarter. Shoulder region and withers very high, and back line from withers greatly inclined toward the rear. Head massive, heavy, relatively short, and set very low.

Thoracic vertebrae 14 and their spinal processes (especially the anterior ones) and those of seventh cervical greatly elongated.

Skull relatively short and broad (basal length only roughly 1.5 times maximum distance between orbits). Frontals well developed, very broad, and moderately bulging. Occipital margin of parietals situated roughly at their center in such a way that they are divided into two parts—smaller facial and larger occipital—with the latter fusing with the occipital bone. Pneumatization of skull considerable. Preorbital depression on lacrimal absent. Ethmoid pit also absent. Orbits project prominently sideways (tubelike) while nasals are relatively short and enlarged in the middle. Horns very small with their tips turned in. Females also sport horns.

Upper molars highly hypsodont with broad crowns and an additional cusp on the inside.

Facial, pedal, and inguinal glands absent. Tail long, reaches calcaneum, and covered with short wool, with a tassel of long hair at the end, and circular in cross section. Hooves narrow, relatively short, and broad. Dewlap present.

---

[29] Maximum height at the withers almost up to 2.0 m and weight up to 1,000 kg; *B. bison* (Anthony, 1928) can be somewhat larger.

These are forest-steppe and steppe, often forest and mountain-forest forms.

The geographic range of the genus is divided into two parts, American and Eurasian. In the first the genus *Bison*, which represents the lone member of Bovini in America, was widespread in historic times, more precisely during the pre-Columbian period (around 1500), although evidently somewhat less than in the Old World. In the north the range extended up to Great Slave Lake or even slightly more northward. The western boundary was formed by the montane region on the west of the mainland, the Great Basin being included. In the south the boundary passed through the upper courses of the Colorado and Rio Grande, south of which the range formed a small projection into northeast Mexico. The eastern boundary of the range ran from Great Slave Lake southeast through Winnipeg and around the Great Lakes to the south. More to the east the boundary of the range formed a small projection into the St. Lawrence river area. The rest of the boundary lay relatively close to the sea coast and the Gulf of Mexico, excluding Florida.

During historic times distribution in the Old World covered western and central Europe, eastern Europe in the north up to western and central parts of the Great Caucasus (see description of wisent below for more details). At present the distribution of the genus has shrunk to a few pockets in preserves.

As pointed out above, all members of Bovini, divided at present into several genera, are very closely interrelated. Their relationship is multifaceted and complex. Genus *Bison* exhibits close affinity with genus *Bos*, i.e., subgenus *Poëphagus* serves as a connecting link between them. On this basis some taxonomists combine the genera *Bos* and *Bison* into a common genus—*Bos*—divided into three subgenera, i.e., *Bos, Poëphagus,* and *Bison*. This point of view has much to commend it. Sometimes the genera *Bos* and *Bison* (when recognized as independent) are combined into a common "group", *Bison*. On the other hand the genus *Bison* is more closely associated with the broad-fronted bulls of the genus *Bibos* (banteng, gaur, and kouprey). The totally free and unlimited successful crossings between the species points to their strong genetic affinity. Buffaloes (*Bubalus* and *Syncerus*) are more isolated.

The genus *Bison* appears in the Upper Pliocene of Asia (*B. sivalensis* and *B. palaeosinensis*; Indian Siwalik formations and northern China). Some forms of wisent from the early Pleistocene, often
388 differing greatly from present-day animals, were widespread almost throughout Europe and the northern half of Asia (even in the New

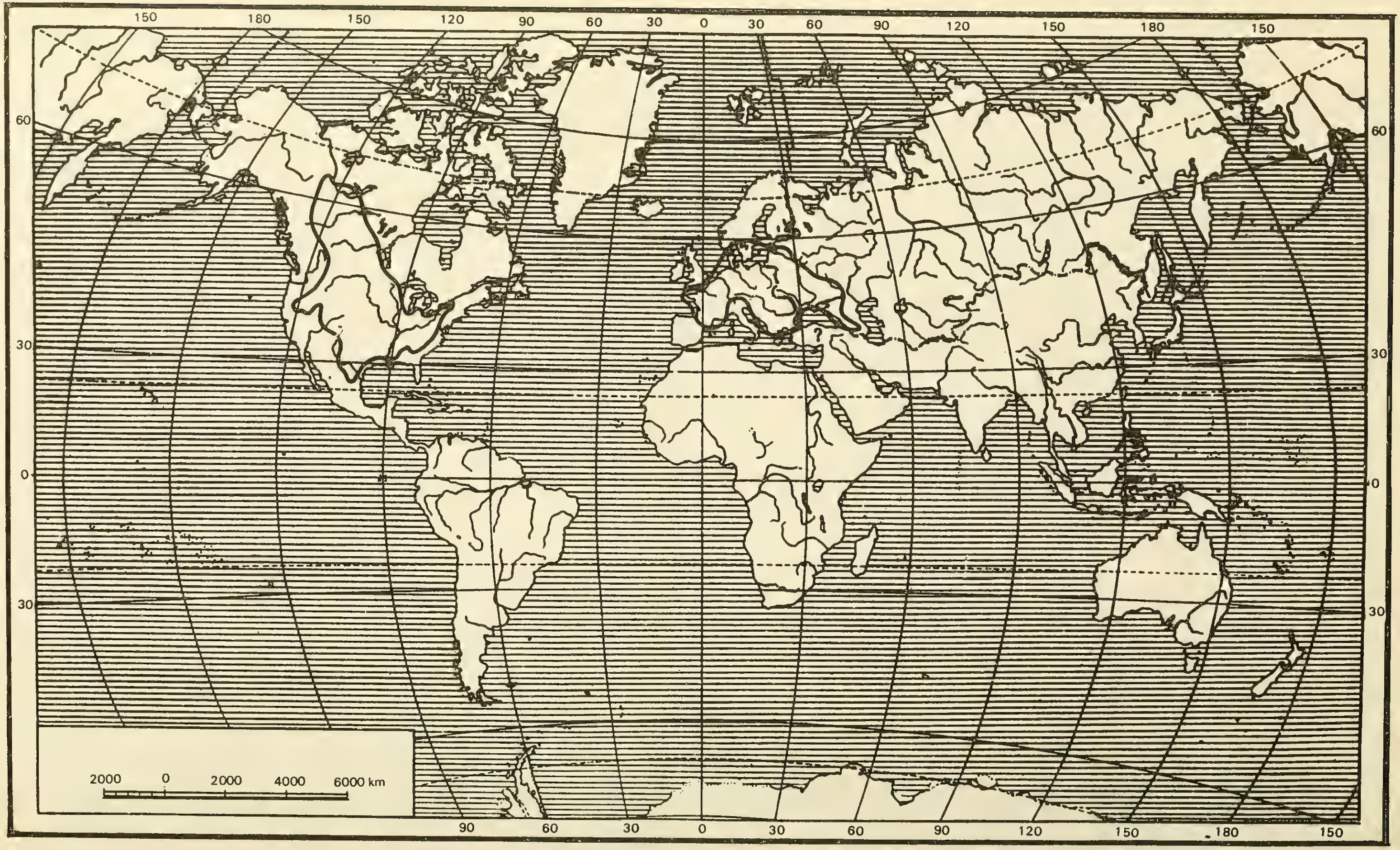

150 180 150 120 90 60 30 0 30 60 90 120 150 180 150
60
30
0
30
2000 0 2000 4000 6000 km
90 60 30 0 30 60 90 120 150 180 150

Fig. 121. Reconstructed geographic range of *Bison* H. Smith (scale in km). American boundary circa 1500. V.G. Heptner.

Siberian Islands). They were represented by only two species: the extinct, very large *B. priscus,* often reaching gigantic proportions, and the present-day *B. bonasus,* representing the diminutive descendant of *B. priscus.* The genus penetrated America in the Pleistocene.

The genus includes two species (10.5% of present-day species of the subfamily)—wisent [European bison] *B. bonasus* Linnaeus, 1758 (Europe and the Caucasus) and bison *B. bison* Linnaeus, 1758 (North America). The two forms are very similar and very close to each other in taxonomic position (freely interbreed and yield viable offspring) but evidently constitute separate species.[30]

At present both species are of no economic importance and are conserved and protected for their aesthetic value. In the past they were important hunting and game animals.

In the USSR one species is found, *Bison bonasus* Linnaeus, 1758 (50% of the species of the genus and 0.3% of all species of Russian fauna). (V.H.)

10. WISENT

Bison bonasus **Linnaeus, 1758**

1758. *Bos bonasus.* Linnaeus. *Syst. Naturae,* 10th ed., vol. 1, p. 71. Evidently Belovezh Forest.

1785. *Bos urus.* Boddaert. *Elench. Animal,* vol. 1, p. 151. 1827. *Bos bison.* H. Smith. Griffith's *Cuvier Anim. Kingd.,* vol. 4, p. 398. Nec *Bos bison* Linn.

1827. *Urus nostras.* Bojanus. *Nova Acta Acad. Carol.—Leopold,* vol. 13, p. 413. Belovezh Forest.

1849. *Bison europaeus.* Owen. *Proc. Zool. Soc. London,* 1848, p. 126. Substitute for *bonasus.*

1903. *Bos bonasus caucasicus.* Satunin. *Zapiski Kavk.* otd. I. *Russkogo Geogr. Obshch.,* vol. 24. Nomen nudum.

1904. *Bos bonasus caucasicus.* Turkin and Satunin. *Zveri Rossii* (Animals of Russia), vol. 4, no. 9, p. 754. Northwestern Caucasus, region of the present Caucasian preserve.[31]

---

[30] The view that Caucasian bison occupy an intermediate position between the European and American bison is unfounded.

[31] An exhaustive description of this form has been given in this work, which is usually credited to Satunin alone. This is quite incorrect. There is no indication in the copy of *Zveri Rossii* (Animals of Russia) with me that the text is Satunin's alone and not that of both authors. Moreover, on p. 754 it is stated that "we . . . acknowledge it (the Caucasian bison; V.H.). . . as a special variety" Greve's name, used abroad (see for example Ellerman and Morrison-Scott, 1951) is undoubtedly a synonym.

1906. *Bison bonasus* var. *caucasia.* Greve *Zool. Beobacht.,* vol. 47, p. 270. Caucasus. (V.H.)

Diagnosis

Bison bonasus is the only species of the genus found in the Soviet Union.

Description

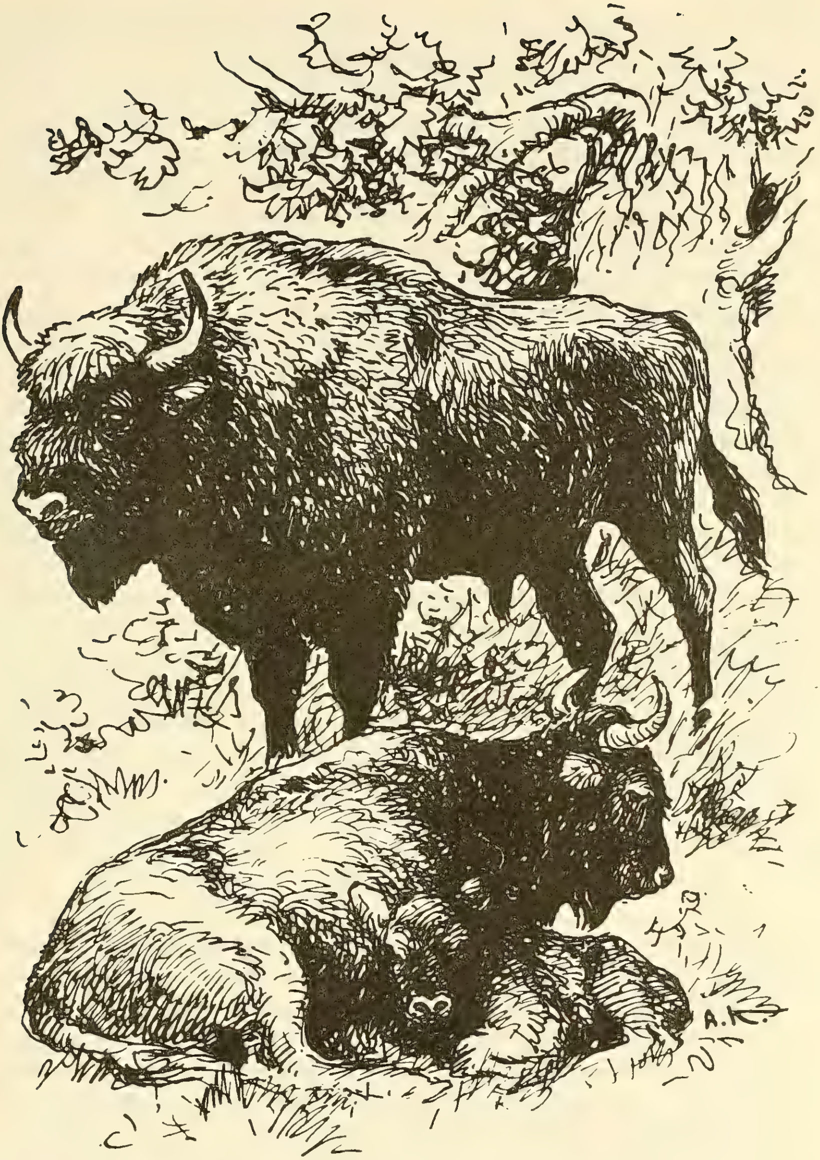
Bull very large, of massive and heavy build. Trunk not long, with a very powerful and massive anterior portion, humped withers, and back greatly inclined to the rear, straight, or slightly curved. Abdomen tucked up. Rear compared to front portion smaller, and front part extends backward in an inclined line middorsally.

Head very large and massive, set low, with a broad forehead of slightly rounded overall shape, largely correlated with the age of the 390 animal. Snout much lower than withers. Head profile appears slightly swollen, forehead broad, and frontal region much broader than muzzle region. Legs powerful and quite long.

Compared to its overall size, horns are very small, relatively and definitely much smaller than those of other species in genus *Bos.* They are set very high (on top of skull) with their bases far apart on the sides of the skull. Horns thick at base, narrowing rapidly toward the tip, circular in cross section throughout, and smooth. On top of skull they initially run straight sideways, then later turn steeply upward and inward, with the tips facing each other. Usually the curvature of the horns lies in the same plane, almost perpendicular to the sagittal plane of the body, but the tips may be turned slightly forward or backward. Keratin of horns pure black.

Eyes small and often covered by hair. Tip of snout between nostrils and top of nostrils bare. Ears short, broad, densely covered with hair, and often hidden in long hair.

Head, except for end of muzzle, neck, withers, shoulders, chest, and upper part of forelegs covered with long curly hair. Head hairy; hair on forehead, between horns, on temples, and occiput particularly long. Prominent beard of long hair occurs under the lower jaw. Tresses of long hair also occur below the neck, up to the chest. Hair on top of neck and on withers sometimes particularly abundant and looks like a mane. Massive growth of entire anterior part of trunk and neck intensifies the impression of bulkiness of the animal, while the dense hair cover on the head, the beard, and the tresses under the throat and neck enhance the impression of heaviness and size of the head.



389 Fig. 122. Wisent, *Bison bonasus* L. Sketch by A.N. Komarov.

Elsewhere on the trunk hair short, straight, and close. Tail covered with short hair with a tassel of long hair only at the very tip. Tail reaches hock. Length of hair greatest in winter and its abundance and length on different regions of the body especially great in winter coat; in summer the hair coat in the region of the withers, shoulders, and partly the neck differs little from that covering the body in the rear.

Color of winter coat dark brown, that of the legs blackish-brown, and that of neck and shoulders somewhat lighter than the body in the rear; latter covered with short hair of a slightly grayish-yellow color. Summer coat shorter than winter, especially in the forebody, and slightly lighter in color. The beard, hair on the head, and the caudal tassel are dark brown in winter as well as in summer. Bare patches on the muzzle and hooves pure black.

Cows are much smaller than bulls, have a less massive trunk, less powerful anterior portion, less developed and lower withers, with a relatively small, less heavy head, which is not as rounded or set as high as in males. Cows have longer legs and are generally more proportionate in build and lighter than bulls. They differ from bulls greatly. Hair growth in cows on the head and other parts of the body is less, although the beard and tresses of hair from the neck are present. On top of the neck and on the withers the hair is longer than on other parts of the anterior half of the trunk. Horns are much thinner and weaker, and usually bent less inward; their tips are directed more upward.[32]

Body length of bulls reaches 300 cm, height at shoulders 185 to 200 cm, height at croup 160 cm, and tail with hairy tassel around 80 cm.[33] Maximum weight reaches 850 kg, probably even 950 or 1,000 kg. The mean weight of Belovezh bulls is slightly more than 500 kg.[34] Cows are far smaller and lighter than bulls. (V.H.)

391 Taxonomy

The wisent, in morphological features, is very close to American bison (*B. bison* L.). The two are also closely related in origin (ancestral form migrated to North America from Asia through Beringia during the Middle Pleistocene). Some researchers are inclined to regard the two as subspecies of a single species and such a view has much to commend it. Yet the number of features distinguishing these two forms is fairly large and there are no "transitional" forms whatsoever between them. At present it appears more correct to consider the wisent and bison as very closely related but separate species. The fact that in captivity they freely interbreed and that hybrids are fertile in spite of complete geographic isolation of the two forms, cannot be adduced in resolving the independence of these species. As pointed out above, geographically continuous species of ox also yield hybrids which are equally fertile. (V.H.)

---

[32] See characteristics of the genus for skull and skeletal features.

[33] Some individuals are even larger. A wisent killed in Germany in 1555 measured 401 cm (? V.H.) in body length 216 cm at the withers, and weight 952 kg. These are the highest known figures (Enar, 1949).*

[34] Data on bulls weighing over 1,000 and even up to 1,600 kg are exaggerations.

*Not in Literature Cited—Sci. Ed.

Geographic Distribution

At present wisent are almost totally extinct and seen nowhere in a natural state.

In the historic past their range covered forest regions of western, central, and partly southeastern Europe, western and southern forest-steppe and partly steppe and forest regions of the European part of the USSR and the Caucasus.

Geographic Range in the Soviet Union

The range in the Soviet Union (reconstructed) was fairly large and constituted a significant part of the range of the species. It covered all of the western and southwestern parts of the country and the Caucasus.

Even in the last century (Usov, 1859 and 1865), wisent were well established and it was firmly believed until recently, in spite of objections (Koppen, 1883), that the European bison was an inhabitant of dense, tall, even wet forests. This view is totally incorrect. It arose as a result of observations on animals living in Belovezh Forest, which turned out to be the last refuge of a dying species driven by persecution by man to conditions not only optimal for them, but even unfavorable. As shown by new ecological data, the results of studies on reacclimatization, and information available on the former distribution of wisent, sparse deciduous forests with glades and open expanses, forest-steppes and even steppes with bottomland deciduous forests, and forests in catchment areas represent the normal habitats conducive for their survival.

"Even in the sixteenth and seventeenth centuries wisent were distributed in Russian forest-steppes from the Dnestr to the Don and were reported at places even in the steppe zone.* Thus wisent were observed in the latter half of the sixteenth century in the Ochakov steppes (Bronevich, 1630) and in the Don Cossack lands in the latter half of the seventeenth century.[35] Moreover, while describing the hunting of ungulates in the Prikumsk steppes in the winter of 1848 to 1849 (Rebrov, 1849) noted that a wisent was caught in 1848, but fails to report the exact place of the catch.

---

*There is no terminal quotation mark in the Russian text—Sci. Ed.

Much information is available on the former distribution of wisent in the forest-steppes. In the middle of the sixteenth century, when Podol'sk was a less-populated area, large herds of wisent grazed in the steppes there. These animals interfered with patrol service of the border regions of Barsk organized by village elders, since they obliterated tracks of Tatar horsemen who were infiltrating the area (Pretvich, 1866). Wisent were common even in the neighborhood of Bratslav (*Arkhiv yugo-zapad. Rossi,* part 7, vol. 1, 1886).

At about the same time (middle of the sixteenth century) herds of wisent were common even in the Dnieper forest-steppes, then under 392 Kiev command. A century later (Boplan, 1660) European bison were sighted in the forest-steppes of the Ukraine near the boundary with Moscow state (the boundary passed close to Glukhov, Putivl, Nedrigailov, Gadyach, Poltava, and along the upper courses of the Orela and Samara). During the 1660's and 1670's Moscow royalty issued orders to the Belgorod regiment to capture wisent in Belgorod, Ostrogozh, and other areas.[36] Apart from Ostrogozh, wisent were present in other places also in the Don forest-steppes, as is evident from the fact that merchants of Moscow state imported hides of wisent from the Don, through the customhouse at Kostenkakh, Voronezh, Uryv, and Korotoyak and by ferrying through Seversk Donets at Svyatykh Gor.

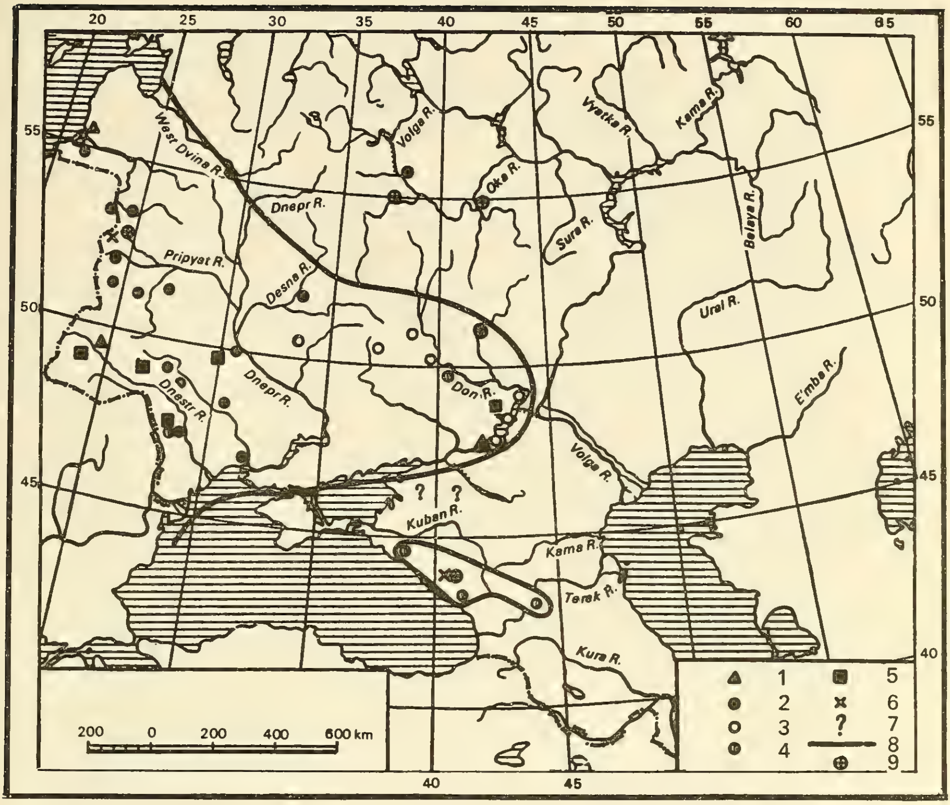
Recent information about the capture and occurrence of wisent in the forest-steppes pertains to the end of the seventeenth and early eighteenth centuries. In 1716 Peter I ordered the Voronezh vice-governor, Kolychev, to capture and send five or six wisent to Petersburg. In response to the order, Kolychev submitted that the animals had last been seen in 1709 near the Don after which they had not been sighted at all (Letter of Peter I to Kolychev, 1785 [*sic*]).

393 Roughly around the same period wisent also disappeared from the left bank of the Dnieper. The animal is mentioned for the last time in that region in a letter by Mazepa written from Lokhvitsa in 1696, in which he notifies the royal palace about a shipment thither of one wisent.

---

[35] *Tsentr. gosud, arkhiv Drevnikh aktov, f. Razryadnyi Prikaz, stolbtsy Belgorodskogo stola,* document 608, p. 91.

[36] *Tsentr. gosud. arkhiv Drevnikh aktov, f. Ostrogozhskaya prikazanya izba,* document 3, pp. 8–9.


20
25
30
35
40
45
50
55
60
65
55
50
45
40
West Dvina R.
Volga R.
Vyatka R.
Kama R.
Oka R.
Dnepr R.
Sura R.
Belaya R.
Pripyat R.
Desna R.
Ural R.
Dnepr R.
Dnestr R.
Don R.
Emba R.
Volga R.
Kuban R.
Kama R.
Terek R.
Kura R.
?
?
200
0
200
400
600 km
1
2
3
4
5
6
7
8
9

392 Fig. 123. Distribution of wisent, *Bison bonasus* L., in the USSR (scale in km). The different signs denote sites for which direct references are available.

1—twelfth century (Pri-Baltic) and eighth to thirteenth centuries (site of old township of Sarkel on the lower Don); 2—fifteenth and sixteenth centuries, and partly the seventeenth; 3—seventeenth century; 4—eighteenth century; 5—areas of distribution about which references are available in literature in a very general way and which pertain to a fairly extensive territory (Galitsk Rus', Kiev command zone, Donsk township, and so on) at different periods but not later than the eighteenth century; 6—nineteenth and early twentieth centuries; 7—probable region of merger of southern Russian part of the range with the Caucasian; 8—probable boundary of distribution in historic times (in the Caucasus during the seventeenth to the twentieth centuries); 9—sites of recent (1958) habitation of reintroduced wisent in semicaptivity or wild state in preserves. V.G. Heptner.

Kantemir in his paper "Descriptio Moldaviae," published for the first time in 1717, reported that wisent were still sighted in Moldavia.

Wisent lived during historic times in the southwestern section of the forest zone of Russia. It is known that in the twelfth century wisent were hunted in the Carpathians, in the territories of the Galician count, Yaroslav Osmomysl. In Volynya in the early fifteenth century wisent were so common that every week about 100 were killed as entertainment by participants to the royal conference convened by Vitovt in 1431.

Farther north wisent lived during the fifteenth to the seventeenth centuries in immense primeval forests: Lyuboml'sk, Ratinensk, Grodnensk, Dovensk, Belovezh, and Perestunsk.[37] The extent to which they were common in these groves can be judged from the fact that all of the 36 divisions into which Perestunsk Forest was divided were based on wisent populations (Volovich, 1867).

Wisent were encountered in northern Lithuanian forests during the twelfth century between Til'zit (Sovets) and Libavaya (Liepaya). The eastern limit of the range of wisent in the forest zone is not clearly known. It is only known that in the middle of the sixteenth century wisent annually swam across the Desna at Novgorod-Severska during their spring and autumn migrations (S.V. Kirikov).

Based on the above data and other material one may conjecture that in the historic past the boundary of distribution of wisent in Russia commenced at the Baltic Sea, probably at the level of the Gulf of Riga (probably even slightly more north, but there is no positive information on this). From the sea the boundary descended southeast, encompassing all of Lithuania and a significant part of Belorussia (some data given above, and on the Chaplinsk township at the beginning of our era; Tsalkin, 1956). It is possible that the boundary included Latvia and a part of Estonia also. The boundary at these latitudes evidently did not extend farther eastward since in excavations at Staraya Ladoga (seventh to the tenth centuries), Novgorod (tenth to the seventeenth centuries), and even at Pskov (from the commencement of our era up to the twelfth century), remains of wisent are absent, although at Pskov, for example, wild boar and roe deer have been found and [red] deer at Ladoga (Tsalkin, 1956).

Continuing farther the boundary bypassed Moscow and Ryazan' to the south (wisent were not discovered in Moscow excavations of the tenth to the seventeenth centuries and excavations at Staraya Ryazan' of the eleventh to the thirteenth centuries) and extended for quite some distance into Kur' and Voronezh districts, encompassed the Don basin, probably from Khoper, and proceeded seaward along the valley. In the south wisent probably reached the coasts of Azov and Black Seas. No information is available about their occurrence in Crimea.

---

[37] These covered immense expanses. The old Belovezh Forest was many times larger than the present area and covered several districts. Lyuboml'sk Grove was west of Kovel, Ratnensk on Pripyat north of it, Perestunsk lay along the Bobr River, a tributary of the Narev, to the south of Lipsk between Grodno and Avgustov.

In literature, particularly in older literature (Brandt, 1867; Dalmatov, 1855; Köppen, 1883; and others), references occur to several former sites of habitation of wisent outside the above limits (Enotaevsk and Dubrovka on the lower Volga, Irgiz River, Syzran', Penza, Spassk Ryazan' province, Orel, Tver (Kalinin), Novgorod, Vologda, Vyatka (Kirov), Perm, and Nizhegorod province (now Gorkii region)). Most of these references are based mainly on excavated remains and pertain to remote periods, beyond the historic past. For the most part, these are Quaternary finds belonging to different forms of wisent. During the Quaternary period these animals were very widely dispersed; Paleolithic animals are known, for example, from the southern Urals, mouth of the Kama, and other places. Some references are definitely erroneous and based on misun-
394 derstandings, for example, references to the occurrence of wisent in the Lykov Forest in the former Semenov region of Nizhegorod province in the first half of the last century (Köppen, 1883).

Nevertheless it is quite possible that the range was somewhat more extensive during historic times. It could have extended farther north toward the Oka and east to the Volga. In other words, the boundary to the east of the Dnieper basin could have resembled more the boundary of the zoogeographic contemporaries of wisent such as western forms of [red] deer, wild boar, and roe deer. It may be assumed that the northern boundary of wisent was determined by the height of winter snows (isolines of snow cover heights in the European part of the USSR run in this very direction) and the eastern boundary semi-deserts (right bank of the Volga), which these animals avoided.

An isolated area of habitation of wisent, somewhat cut off from the one described above, was found in the Caucasus. Information about this region is extremely scanty and pertains only to the eighteenth, nineteenth, and early twentieth centuries. Only stray information is available for the earlier historic period. During this period the geographic range in the Caucasus encompassed the forest zone on the northern slope of Glavnyi [main] range and its foothills ("Chernye gory") from its western extremity in the region of the Pshekha and Pshish River (running northward from the divide above Tuapse) and at least up to the Urukh (left tributary of the Terek) in the east; it is highly probable that it ran even up to the Georgian Military Highway.

The animals lived only in the extreme western part of the southern slope of Glavnyi range up to the frontiers of then Abkhaz and Mergrelia. They occurred in the Abkhaz range and in mountains above Sukhumi.

From the middle of the eighteenth century, the period to which the above data for Abkhaz pertains, the area of habitation of the animal was rapidly reduced. In the Urukh basin they disappeared evidently during the early nineteenth century itself, at which time they were also absent along the Teberda. By the end of the nineteenth and early part of the twentieth century, wisent were preserved only in forests of the upper courses of the Kuban (Laba, Belaya, and Urup) in the territory of the present Caucasian preserve formerly set aside for royal hunts. The last of the Caucasian bison was killed there by poachers in 1926.

There is no doubt that wisent lived on the Caucasian steppes also and that their geographic boundary here was contiguous with that of the Don steppes and Don valley. This is supported by the discovery of wisent remains belonging to the Middle Ages in Sarkel fort along the lower courses of the Don at Tsimlyansk Cossack village (eight to the thirteenth centuries). How and when this link was broken is still not clear but it probably occurred at a much later period. This is suggested by information cited above on the occurrence of wisent along the Don. Yet reports about the capture of a wisent in 1848 in the Prikumsk steppes evidently cannot be taken as proof of the existence of this genus in that region. They could refer to an animal which had emerged from the forests into the foothills. There is no doubt that wisent did not inhabit the Cis-Caucasian steppes in the first half of the last century.

In the remote prehistoric period wisent were present in the Caucasus and dispersed even more widely in Cis-Caucasus. Remains are known from dwellings around Lake Sevan (3000 B.C.). During this period and slightly later (Bronze Age), wisent were not rare in northern Armenia and the steppes of the Cis-Caucasus.[38]

The following is a more detailed picture of the distribution and disappearance of wisent in the Caucasus. According to Vereshchagin and Naniev (1949) "skull 'collections' from Ossetian sanctuaries belonging to the sixteenth through the nineteenth centuries point to the occurrence of wisent on the undulating plains now divested of forests and in the mountains of central Cis-Caucasus." Of the 18 sanctuaries, wisent skulls have been found in 4: upper and

---

[38] Data on the distribution of wisent in the Caucasus are from Ruzskii, 1898; Dinnik, 1910; Vereshchagin and Naniev, 1949; Bashkirov, 1940; and others; and also based on material from S.V. Kirikov.

lower Lesgora, Digorized cave, and Dunta—all situated in gorges of
395 the Urukh River and its tributaries (79 skulls). Moreover, Satunin (1914) recalls that bison skulls have been found even in Rekom sanctuary in Ossetia, but it is quite possible that this refers only to the note by Pallas (1811) about the reported sighting of skulls in the Rekom gorge by Digory Güldenstädt. In any case wisent remains were not found in 1947 while specially processing the collection from Rekom sanctuary in Ardon gorge (Vereshchagin and Semenov-Tyan-Shanskii, 1948).

Information is available in literature about the presence of wisent in the Caucasus from the Middle Ages. Rashid-Ad-Din (sixteenth century; 1946) reported that Abagā-Khan while wintering in 1275/1276 in Aran, five farsangs [a Persian unit equal to about four miles] from Shakhrud, hunted for "mountain buffalo" in the forests. In describing the hunt of Gazan-Khan in Talysh during 1301 to 1302 the same historian (Ibid., pp. 188 and 189) noted: ". . . after this war, soldiers organized raiding parties and chased wild animals such as mountain buffaloes, dzhurs, wild goats, donkeys, foxes, wolves, bears, and all other types of wild animals and predators into pens . . . ." "Dzhurs" probably refers to roe deer ("dzhuyur" in Azerbaidzhani) and wild goats to bezoar goats or goitered gazelles.

Stories about the occurrence of some kind of wild bulls in the Talysh and Elburz mountains persisted even up to the nineteenth century (Menetrie, 1832). Brandt's critical review (1867) of this subject provided no new data. It is possible that the disappearance of wisent in the forests of Elburz and Talysh coincided roughly with that in the forests of central Caucasus, i.e., during the Eighteenth and nineteenth centuries.

The first references in literature to wisent in Cherkessia are possibly those of John de Luke (1625) and in Abkhazia of Archangelo Lamberti (1654).

Wisent raised in Kabarda, Ossetia, and Ingushetia were known in Moscow long before Academicians Lovich, Güldenstädt, and others came along; nevertheless, the first two authors are generally regarded (Bashkirov, 1940) as the original discoverers of wisent in the Caucasus.

In Order 21 (1739) of "Polnyi sobraniya zakonov Rossiiskoi imperii c 1649 goda" [Complete Collection of Russian Imperial Laws from 1649] (vol. 10, 1830, p. 7994) a reference occurs to a personal order issued by the cabinet of Her Imperial Majesty, Anna Ioanovna, to the Astrakhan' deputy commander "to capture and dispatch various wild animals to the palace and Izmailov menagerie every year . . . We know that in Kabarda there are wild bulls and cows locally known as 'dombai'. You are expected for this purpose to do your best without consideration of expenses from our treasury, so that the local count can place at our disposal bulls and calves 5 to 10 weeks of age by capturing them and sending them to Kizlyar Fort. There the animals shall be fed on bread and upon acclimatization sent to Astrakhan' by river and from there to Moscow along with other animals, and you yourself should write to Shamkhal Gorskii, and also to the commandant of Kizlyar Fort and Elmurze Cherkaskii, so that they can assist you in the capture and shipment of said bulls and calves . . . ."

It is possible that wisent were present in Chechna and Northern Ossetia even during the travels of Güldenstädt, i.e., 1770 to 1774. Dinnik (1890) even found some older inhabitants of Zedelesk village who related accounts of their ancestors shooting wisent with iron bullets. One skull found in Digorized cave bore the inscription "1833," possibly denoting the data of death of one of the last wisent in Ossetia.

By about the middle of the nineteenth century wisent had escaped extermination only in the mountains and forests of the northwestern Caucasus. The gradual disappearance of wisent in this region occurred in several stages. In the middle of the nineteenth century the northern boundary of distribution of wisent paralleled the latitude of the Cossack villages Dagestansk and Abkhazsk. The eastern boundary was probably represented by the longitudinal course of the Kuban right to the mouth of the Malyi Zelenchuk. In the west wisent reached Pshish creek. Based on a comparison of local folklore, Bashkirov (1940) concludes that wisent at that time possibly inhabited the upper reaches of the Shakhe, Sochi, Mzymta, Psou, Bzyba, Kodora, and Ingura rivers. The overall population of wisent in the 1870's have been reckoned as over 2,000 animals.

396 The growth of the Caucasian war and the colonization of the foothills by. Caucasians gradually drove wisent into the region between the upper reaches of the Beloe and Laba. Increased cattle husbandry, cutting and clearing of forests, and hunting gradually reduced both the population and area of distribution of this animal. By the 1890's the population of Caucasian wisent was reckoned as 500 to 700 (Satunin, 1898), even 442 (Kulagin, 1918).

During the 1890's Kuban Great Imperial Hunting Grounds, which extended over an area of 522,000 desyatins* of wisent country, took measures to ward off poachers, which largely arrested the decline of wisent. Special studies by Filatov (1910 and 1912) nevertheless reveal that the area in which wisent survived was reduced. In Filatov's map wisent are distributed only between the upper reaches of the Beloe and Great Laba. The wisent population was placed by Filatov in 1910 at a few hundred (Bashkirov, 1940). (N.K. Vereshchagin).

---

*Desyatin = 2.7 acres—General Editor.

By 1917 the number of wisent evidently did not exceed 500. Innumerable herdsmen invaded the Kuban hunting grounds, forests were felled, and hunters equipped with sharp weapons—all had a devastating effect on the population of Caucasian wisent. "Most of the animals were killed in no time for their meat and hide. In 1919 some epizootic disease raged among the remainder, probably transmitted by domestic cattle. By 1920 the population was reduced to 50 animals, including not less than 20 in the region of Kisha-Khamyshka. Wisent hunting by poachers continued even later.

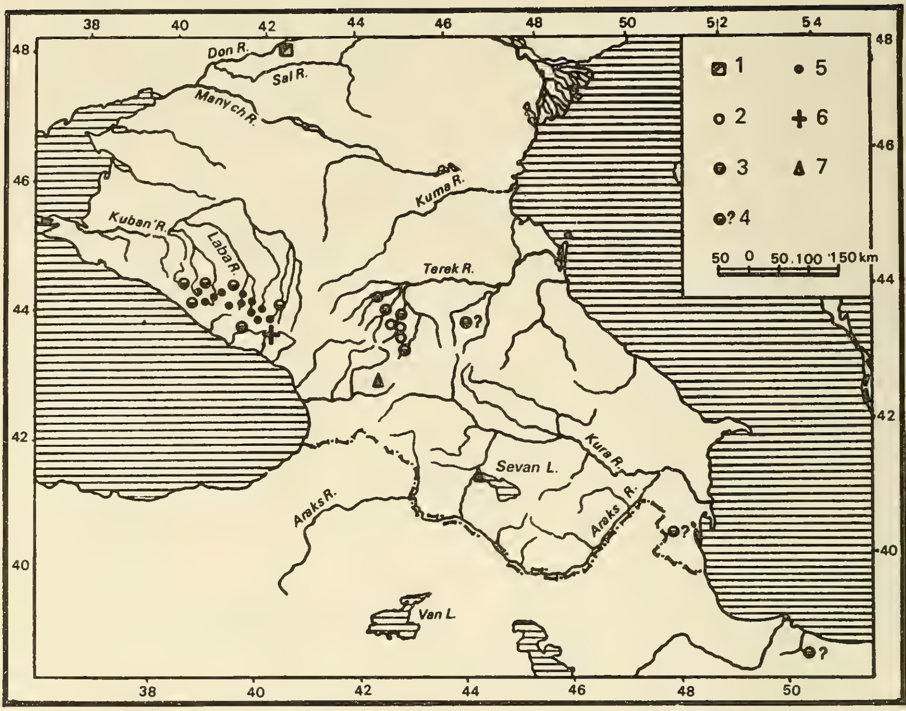
"The formation of the Caucasian preserve in 1924 could not save wisent because of difficulties of protecting them in the hills and the 397 availability of long-range weapons to the local people. From 1921 through 1925 killing of wisent was recorded near Lineinaya Cossack village, 50 km west of Maikop (1921), near Gefor Mountain (1923), and in the upper reaches of the Kodor (1925 and 1926) at Alousa and Mastakana. On Alousa Mountain Imeritian herdsmen [of Georgia] killed in 1926 three wisent, probably the last of the animals to survive there. Anyway no further information about wisent could be found thereafter (Bashkirov, 1940)". (N.K. Vereshchagin). The history of restored wisent dates in the Caucasus from 1940.

At the commencement of the First World War wisent in Russia survived in a wild state only in Belovezh Forest and, as pointed out above, in the upper reaches of the Kuban. Moreover, there was a small group of Belovezh animals in the game park at Gatchin near Leningrad, in the Tzar's hunting grounds in montane Crimea in the region of the present Crimean preserve, and at Askaniya-Nova on the Fal'ts-Fein farm. All these animals died either during this War or the Civil War. The small group surviving in Belovezh Forest was removed to Germany.

As a result of the work on restoration of wisent, in spite of heavy losses during World War II, a fairly large number of pure-blood and high-blood [hybrid] wisent are now available in the Soviet Union (on January 1, 1960). These are confined to Belovezh Forest (45 animals), Priok-Terras preserve near Serpukhov (central bison nursery; 35, 9)*, Mordov preserve near the city of Temnikov (2,18),

---

*The two numbers in parentheses probably refer to the number of purebred, and hybrid animals; see below **(pg. 574 ff)—Sci. Ed.**



396 Fig. 124. Places of sightings of Caucasian wisent, *Bison bonasus caucasicus* Sat., in the Caucasus and some adjoining territories (scale in km).

1—finds in the eighth to the thirteenth centuries; 2—material collected from literature for the fourteenth to the eighteenth centuries (Ossetian sanctuary); 3—references in literature for the fourteenth to the eighteenth centuries; 4—dubious data given in literature for the same period; 5—habitats in early twentieth century; 6—hill sites of the last native Caucasian bison (1926); 7—Holocene finds. N.K. Vereshchagin.

Khoper preserve on the Khoper near Borisogleb (3, 19), Caucasian preserve (12, 19), and Oka (2). In Caucasian preserve the animals live in total freedom and elsewhere in large pens or in partial freedom.

Geographic Range outside the Soviet Union

The range outside the Soviet Union once included France (the animal became extinct in the sixth century), Holland, Belgium (survived even at the commencement of our era), Germany (became extinct in Saxony in 1793), and Pri-Baltics (the last of the animals was killed in 1755[39]). Wisent inhabited Denmark, Poland, southern

---

[39] Between Labiau and Til'zit in Neman (Lydekker, 1912), i.e., between present Poles'e (Labiau) and Soviet Kaliningrad district.

Sweden, Hungary, Czechoslovakia (Carpathians), Rumania (the last of the animals was killed in Radnansk mountains in 1762; it survived in Transylvania probably up to the end of that century), Switzerland, and the Balkan Peninsula in the south to Frakia and Macedonia. In the Balkans (Greece) wisent were destroyed very early, probably on the threshold of historic times, and became extinct in northern Spain even during prehistoric times, as in England. In central Europe wisent were widely distributed at places in the fifteenth and sixteenth centuries. (V.H.)

Geographic Variation

In the absence of adequate material it is now impossible to judge the geographic variation of the species in the remote past, when it was widely dispersed throughout Europe. Based on theoretical premises geographic variability probably was not expressed. However, differences among European wisent, viz., between those of Belovezh Forest and Caucasian populations, until the early twentieth century were quite real and there is justification for recognizing two subspecies of this group.[40]

1. European (Lithuanian) wisent, *B. b. bonasus* Linnaeus, 1758 (syn. *urus, nostras,* and *europaeus*).

Very large animals. Bulls stand about 185 cm at shoulders. Weight of adult bulls up to 850 kg with an average of 500 to 515 kg (32 poods). Hooves elongated. Length of central hooves of forelegs in an adult bull 90 to 105 mm and of lateral hooves 40 to 50 mm; length of central hooves of hind legs 100 to 115 mm and of lateral 40 to 55 mm. Hair throughout body nearly straight or slightly curly, longer on the sides in pelvic region. Hair on anterior part of body relatively long. Length of beard up to 370 to 400 mm and length of 398 hair below neck 180 to 250 mm. Color very light, brownish with an ocherous-cinnamon tinge.

This subspecies survived in the European part of the USSR probably up to the Don, and even up to the Cis-Caucasian steppe. Outside the USSR, it was confined to central and western Europe.

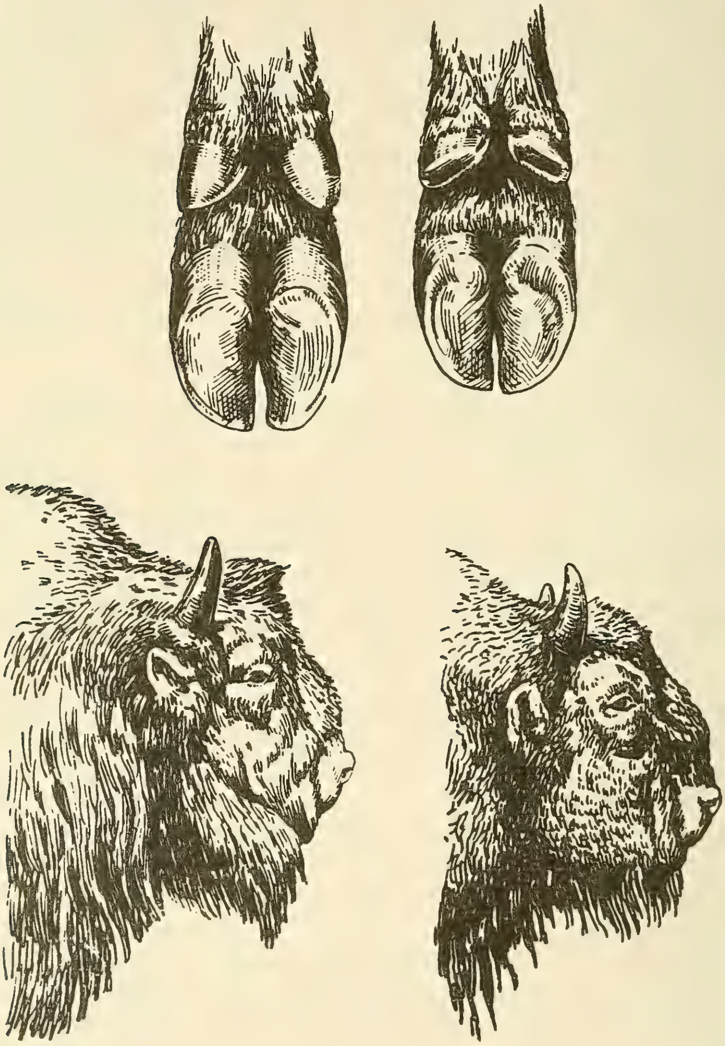
2. Caucasian wisent, *B. b. caucasicus* Turkin and Satunin, 1904 (syn. *caucasius*).

Smaller than Lithuanian wisent; height at shoulders 160 cm. General build also lighter. Weight up to 700, in rare cases 800 kg, with an average of 480 kg (28 poods). Hooves shorter, higher, and rounded. Length of central hooves of forelegs in an adult bull 70 to

---

[40] Diagnostic features from Flerov (1932), with some minor changes included.

85 mm and of lateral 25 to 35 mm; corresponding measurements for hind legs 75 to 90 and 25 to 35 mm. Body hair curly throughout, locks on body set steeply, more prominent on head and neck. Hair cover on anterior body short. Length of beard not more than 250 mm and on lower part of neck about 150 mm. Color dark cinnamon-brown with a chocolate tinge. On head, neck, and legs long hair sometimes turns black.



398 Fig. 125. Heads and hooves of Lithuanian wisent, *Bison bonasus* L. and Caucasian wisent, *Bison bonasus caucasicus* Turk. and Sat. (from Flerov, 1932).

399 This subspecies inhabited the northwestern Caucasus in the last century. It did not exist outside the USSR.

The light build, lesser weight, and structural features of the hooves are typical features of mountain animals.

It is sometimes pointed out that the characteristics of Caucasian wisent render it somewhat an intermediate form between the [European] wisent and [American] bison. There is absolutely no justification for such an assumption. (V.H.)

Biology

The destruction of wisent proceeded much faster than their study. Many aspects of their biology in natural habitats have, therefore, remained vague and even obvious contradictions in descriptions by various researchers remain unresolved. Observations made at later periods on purebred and hybrid wisent raised at some places in the USSR have brought us nearer to an understanding of the main features of the biology of the species, but great caution must be exercised in using these data to formulate the characteristics of these animals in the natural state. In their conditions of survival and sometimes in their pedigree present-day wisent cannot be regarded as totally identical with extinct primitive wisent. Even the habitats of wisent have undergone drastic changes over the past decades.

Population. The natural habitat of wisent during the early part of the twentieth century was limited to Belovezh Forest and the western Caucasus. In 1902 in the region of Belovezh Forest (about 138,000 hectares) there were 750 ± 20 wisent (Kartsov, 1903); by early January, 1914, they numbered 727 (Vrublevskii, 1927). This number includes wild animals as well as a small number held in captivity. In 1915, with the advancing War front, captive wisent were set free. In that year a large number were destroyed; moreover, 15 wisent were taken to East Prussia. There remained in the Forest 178 to 200 bison in 1916; 121 in 1917; 9 in the winter of 1919–1920; and a lone female at the end of 1920; the latter was killed in February, 1921 (Vrublevskii, 1927; and others).

The wisent population of the western Caucasus was never studied as well as that of the Forest. According to Dinnik (1910) in the first decade of the twentieth century there were several hundred Caucasian wisent, most probably 500 to 600. Their distribution during those years was confined to the Kuban Game Park (522,000 hectares). According to Filatov (1912) wisent numbered 100 to 1,000, probably several hundred. Pfizenmayer (1929), who had at his disposal the data of Yutner, the former director of Kuban Game Park, estimated their population for the 1890's as 400, and 600 for the year 1910. As soon as the Kuban Game Park ceased functioning, the destruction of wisent proceeded at a rapid tempo. During the years of World War I and later during the Civil War, much of the wisent population died out or was destroyed by epizootic diseases. By 1924, when the Caucasian preserve was instituted, only some 10 to 15 wisent were left (S.A. Severtsov, 1926); the last wisent was killed by poachers in 1926 or 1927.

Of the several young wisent imported at different times from the Caucasus into Germany during 1907, only one male produced offspring (by crossing with a Belovezh wisent). This parent wisent died in 1925 but its offspring were used for restoring Caucasian wisent through selective cross-breeding.

Wisent were exported regularly from Belovezh Forest. In the midnineteenth century several wisent were brought to Tsarskoe Selo, and were later sent to Gatchina Game Park. In 1902 there were 19 wisent there (Kartsov, 1903) and in 1917, 36; in that year they were destroyed. In 1865 Belovezh wisent were exported to Pshinsk Game Park owned by the Duke of Pless in Upper Silesia (Kartsov, 1903). Wisent were sent there several times and totaled 74 before World War I. The offspring of these animals are preserved even today.

400 Belovezh wisent were also sent to the Pototsk Game Park "Pilyavin" (Western Ukraine) where there were 22 of them in 1917; in that year, however, they were all destroyed.

In 1902 a beginning was made in raising wisent in Askaniya-Nova by importing a pair of Belovezh animals. These wisent were also crossed with Ukrainian horned cattle; experiments were conducted in 1933 in the Askaniya-Nova branch at Burkutakh (Lower Dnieper; Zablotskii, 1939). In 1941 the number of Askaniya hybrid wisent exceeded 50. In the latter half of that year all the local wisent died.

In 1913 four Belovezh wisent were introduced into the Crimean preserve. There they multiplied to nine by 1917. Between 1917 and 1919, however, they were killed by poachers (Rozanov, 1931). Wisent were imported again into Crimea in 1937. On this occasion five hybrids were brought from Askaniya-Nova and released in the Crimean preserve in a pen close to the place where the former batch had been held (Bashkirov, 1939). During the occupation of Crimea by the fascist army these wisent were destroyed.

In 1940 five hybrid wisent[41] were brought from Askaniya-Nova into the Caucasian preserve and held in a pen on the right bank of

---

[41] Among these were a male and female with the blood of Caucasian wisent.

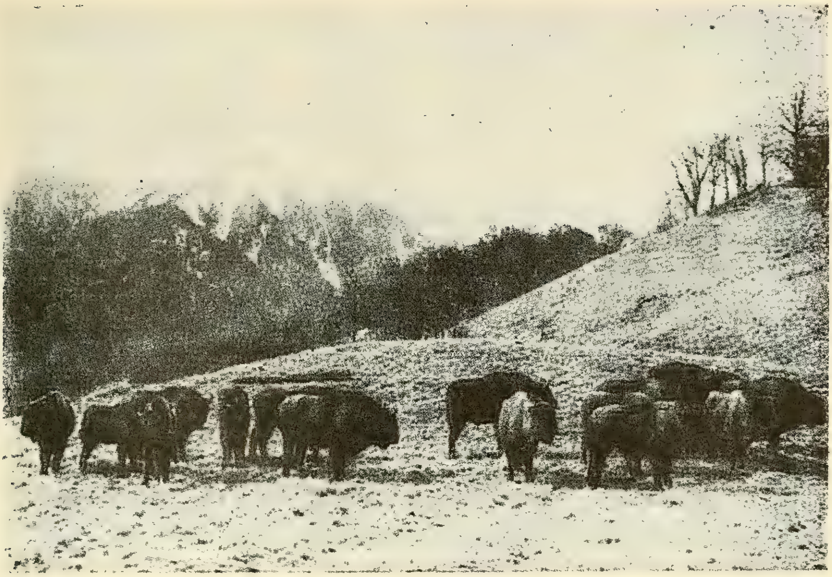


Fig. 126. Wisent in Shirokaya glade (Kishi basin) in Caucasian preserve. Photograph by V.N. Aleksandrov.

the Kishi River. By 1946 the herd had multiplied to 11 animals (Krainova, 1947).

From 1929 to 1936 a total of 12 wisent were imported into Belovezh Forest (mainly from Germany); of these 8 were purebred and included Belovezh, Caucasus, and Pless lines. Held in a pen, by the end of 1941 this herd had multiplied to 21 animals. In spite of poor maintenance conditions during the years of World War II, mortalities, and poaching (in 1943 and 1944 the wisent were released from the pen), some of the animals bred. At the end of World War II, 17 survivors were gathered into the wisent nursery of Belovezh Forest (Poland) (Zablotskii, 1947).

401 From 1946 onwards wisent were raised in the USSR section of Belovezh Forest. For this purpose five of the Caucasian line were imported from Poland[42] and placed in a pen in Belovezh preserve. Subsequently the wisent herd enlarged, partly through multiplication and partly through importation of new animals, including

---

[42] Polish wisent were imported into the USSR several times thereafter. By 1955 in all 19 bison had been imported, including 10 in Belovezh Forest 7 in the central bison nursery near Serpukhov, and 2 in Caucasian preserve (*Gosudarstvennaya plemennaya kniga zubrov i bizonov*) [State studbook of wisent and bison].

forms from Poland. In 1953 six young wisent were released from the pen as an experiment (Sablina, 1955).

Likewise, the herd in Caucasian preserve grew not only by multiplication, but also by imports from different regions of the USSR and from Poland. Later, a second bison nursery was organized in the Caucasian preserve and at Umpyr' on the Malyi Laba River (1952), in which some wisent from Kishi were kept. In subsequent years wisent in the Caucasian preserve were freed. They were provided with hay in winter.

In 1948 near the town of Serpukhov in Moscow region, a central wisent nursery was organized at Priok-Terras preserve. The herd comprised wisent imported from Poland and other Soviet preserves. In the 1950's some of these animals were semifreed.

In 1955 wisent were introduced into Khoper preserve (from Priok-Terras preserve and Belovezh Forest), and in 1956 into Mordov preserve as well (from Priok-Terras preserve). Wisent were also introduced into the Nal'chik region.

For purposes of breeding wisent of desired lineages, to enhance their pedigree, to control the sex composition of the herd, etc., wisent were transferred from one preserve to another at regular intervals. Inside preserves the animals were held in the following

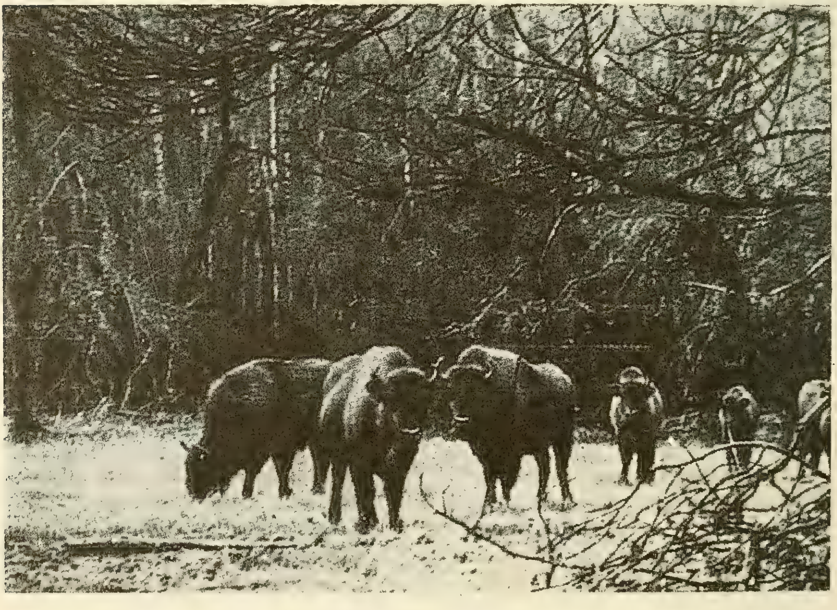


Fig. 127. Wisent in Umpyr' wisent park. Caucasian preserve. Photograph by V.N. Aleksandrov.

manner: freely roaming, stallfed and grazing, grazing in pens, and pasturing (Zablotskii, 1957).

402 On January 1, 1957 there were 69 purebred bison and about 150 hybrids (mainly wisent-bison hybrids) in preserves and zoological parks of the Soviet Union. Among the purebred animals, 24 (13 males and 11 females) were of the Belovezh lineage and 45 (22 males and 23 females) the Caucasian mountain subspecies (Zablotskii, 1957; and others). The population size and distribution of wisent on January 1, 1958 are shown in Table 4.

TABLE 4. DISTRIBUTION OF WISENT, BISON, AND THEIR HYBRIDS IN PRESERVES AND ZOOLOGICAL PARKS OF THE SOVIET UNION ON JANUARY 1, 1958 (FROM DATA OF M.Z. ZABLOTSKII)

Preserve or zoological park	Wisent	Bison	Wisent-bison hybrids	Complex hybrids	Total
Priok-Terras	24	2	—	8	34
Caucasian	5	—	131	—	136
Khoper	2	—	—	7	9
Mordov	2	—	—	6	8
Belovezh Forest	39	—	—	—	39
Askaniya-Nova	1	9	—	1	11
Zoological parks[1]	6	8	10	19	43
Total for the USSR	79	19	141	41	280

[1] Animals are kept in zoological parks in 20 towns, with the maximum held in Riga (11) and Alma-Ata (7).

Habitat. Belovezh Forest, where the European subspecies of wisent (*Bison bonasus*) has been preserved longest, is a large swampy forest massif interspersed with low (125 to 130 m, rarely higher) hillocks covered with pine forest admixed with other species of trees (fir, oak, and birch). The lower and wetter "uplands" are covered with deciduous forests of oak, hornbeam, aspen, ash, maple, elm, and others; places of this type are called *grudi* [heaps]. Much of the territory consists of extremely wet lowlands between the hillocks, which are overgrown with alder, ash, partly oak, and other trees. This is a very hummocky area abounding in wind-felled trees; sections which are depressed most are covered with marshes and often swamps. The rich herbaceous vegetation in the wet lowlands remains green for a long time. Attracted by abundant food and protective conditions, wisent remain in these lowlands from midsummer to late autumn (Vrublevskii, 1912 and 1927). In the earlier part of the year these areas are flooded with snow melt waters, as a result of which the growth of grass is greatly inhibited.

In spring, following floods, wisent graze in floodplain meadows where fresh green vegetation begins to emerge earliest. The animals remain here for 1.5 to 2 weeks, migrating thereafter to the tops of hillocks, first into pure pine forests, and somewhat later into pine forests with an admixture of oak and other deciduous species. In June "heaps" serve as grazing grounds and later wet lowlands between the hillocks. Such a habitat-related dispersal of wisent is mainly attributable to the sequence of the receding snow cover and the growth of young green shoots. Hence during the warm season of the year the animals select such areas where maximum fresh food is available. In autumn they readily move into hay-fields and trample them, visit places of harvesting, and move to winter wheat fields (Kartsov, 1903; Kulagin, 1919; Vrublevskii, 1927).

The winter concentration of wisent in different sections of the forest is determined by the availability of hay and other supplementary food. However, the animals prefer those sections of the forest with maximum underbrush and tender undergrowth; here, they 403 readily visit overgrown clearings. They are also attracted to places of recent wind-felled trees where abundant arboreal lichens are available (Kartsov, 1903; Kulagin, 1919).

The migrations of wisent in Priok-Terras preserve, at present, are similar to the above-described habitat-related movement of animals during the warm season in Belovezh Forest. Wisent gather in spring, summer, and autumn in areas with abundant fresh food during these periods (herbaceous vegetation of early phases, puddles, and tender leaves) and in winter in areas with an abundance of acorns, mushrooms, and leaves of undergrowth and shrubs (Zablotskii, 1957).

Belovezh Forest is the relict of a once extremely extensive range of European wisent. Living conditions for wisent there were evidently far from optimal (Wroblewski, 1912 and 1927; Zablotskii, 1957). Wisent were preserved there, however, only because the forest massif was not felled and, right from the first half of the sixteenth century, they were regarded as an object of hunting for the more privileged aristocracy and thus were protected. There is no doubt that the habitational distribution of European wisent was altogether different in other sections of the range.

The habitat of Caucasian wisent (*B. b. caucasicus*) and their biology have been detailed by Dinnik (1884, 1897, 1902, 1910, etc.) and Filatov (1910 and 1912). Dinnik's observations took place mainly in the last two decades of the nineteenth century and the commencement of the twentieth century; Filatov did his study almost a decade later (1909 to 1911). The environmental conditions for wisent in the western Caucasian mountains underwent a complete change in those years due to utilization of this region for pastures and forest-based industries (felling of trees and production of battens and wooden barrels), which explains some of the contradictions in the descriptions given by Dinnik and Filatov.

Wisent were confined in the mountain range to 900–2,100, but were sometimes sighted at lower or higher levels. Tracks were detected in the mountains at heights of over 2,100 m even at steep places, a few kilometers away from the forest; in the upper reaches of the Abago (Beloe basin) wisent tracks and feces were discovered at a place under a high mound of snow in summer.[43] Wisent tracks were invariably detected on lower alpine meadows in summer.

A favorite place for the summer residence of wisent was the region of upper forests formed of deciduous species, i.e., mountain maple and birch. Subalpine pastures of tall grass remain fresh right up to autumn. They are often bordered with rhododendron shoots through which bison find it difficult to sneak stealthily. Thanks to relatively low temperatures, mosquitoes, midges, and gadflies are totally absent in such pastures on many days.

From there, wisent moved on to graze in lower alpine meadows, sometimes descending even into the region of boreal forest, mainly fir, and in Bol'shoi Laba basin, also spruce. Many wisent spent much of the summer in fir forests, congregating there near glades overgrown with tall grass. Wisent avoided rocky sections (Dinnik, 1910; and others).

According to Filatov's observations the summer distribution of wisent was confined to the fir forest belt from 1909 to 1911; the main grazing ground was the tall grass glade in the forest and the slopes of gorges luxuriantly overgrown with cow parsnip and coltsfoot. These sections usually provide excellent shade and insects there are relatively less troublesome as long as the weather is not very warm. Wisent moved to subalpine and low alpine meadows only in spring and early summer up to the arrival of cattle. Filatov himself never saw them there even once, however.

Thus in the years of Filatov's observations the summer habitat-related distribution of wisent had changed considerably compared to the period of Dinnik's travels. Changes were greatly due to human
404 factors in Filatov's time. Wisent could visit subalpine and low

---

[43] Rossikov (1890) saw in summer the tracks of a wisent in a fern field in the region of Sanchar pass (upper Bol'shoi Laba River).

alpine regions only in spring since shepherd families and numerous cattle were present in summer. Trees were felled in the lower sections of the boreal belt and broad-leaved forests in the region of Kuban Game Park and forests along rivers also cleared (Beloe and Bol'shoi and Malyi Laba).

Data on the winter ecological distribution of Caucasian wisent are extremely scanty. Filatov visited the western Caucasus in the low snow winter of 1909 to 1910, which was, however, not typical of this locality. In that winter (December-January) wisent were present relatively high in the upper half of the boreal belt of the forest. In winters of normal snow the main wintering sites of wisent were the lower section of the boreal belt and broad-leaved forests (Nasimovich, 1939), but wisent had already been displaced from the latter places by the end of the decade. In the 1870's wisent visited broad-leaved forests in the winter much more frequently; some animals were found in the mountain range below 500 m. It is possible that individual animals occurred there in summer also, but this is based on indirect information (Bashkirov, 1939).

The ecological distribution of wisent must have been altogether different on the northern slopes of the central Caucasus (Kabardino-Balkariya and Digoriya), where this species became extinct in the eighteenth to the early nineteenth centuries and at places even earlier. In this Caucasian boreal region vegetation was practically absent in the mountains and broad-leaved forests were often immediately bordered with subalpine meadows or changed into a pine forest. Wisent there were evidently confined to beech and hornbeam forests and also to river valleys overgrown with tall grass (Vereshchagin and Naniev, 1949). Almost nothing is known about the habitat of bison on the southern slopes of the Glavnie Caucasus range in the western Trans-Caucasus, where small numbers of these animals were sighted in the nineteenth century.

Under the free-living conditions permitted at present in Caucasian preserve, wisent are confined to the mountain belt from 700 to 2,400 m (Kalugin, 1958). However, wisent enter open expanses of subalpine and alpine meadows less eagerly than tall grass glades in the upper forest belt. In summer they graze very well in the upper forest belt and in the avalanche troughs in the boreal forest with subalpine vegetation. Wisent also consume the leaves of trees bent down to the ground (Zablotskii, 1957).

Food. The diet of wisent has been studied little in the past. Summarizing all the important eyewitness accounts of food of Belovezh and Caucasian wisent yields a list of only 50 plant varieties, seasonally far fewer.

According to Filatov (1910 and 1912), Dinnik (1910), and others, Caucasian wisent fed in the warm season mainly on herbaceous vegetation, avidly consumed coltsfoot, buttercup, touch-me-not (*Impatiens*), and fescue and brome from among grasses. Often they consumed ferns[44] and leaves of blackberry and cow parsnip (*Heracleum*). Browse especially barks of trees, including mountain ash, elm (*Ulmus montana*), fir, and other kinds, were consumed even in summer, but in a smaller quantity than in winter and spring. The animals gnawed at the bark of fallen fir trees (sometimes they also consumed rotten wood) and roots protruding out of the soil.[45]

In autumn they probably consumed wild berries and pears, which are abundant in the Caucasus (Bashkirov, 1939); these data are confirmed by observations on present-day wisent in Caucasian 405 preserve (Krainova, 1951). No information is available about the intake of acorns and beechnuts by primeval wisent in the Caucasus.[46]

In winter and spring browse foods were of utmost importance for wisent. Bark intake has been reported time and again, probably because the intake of shoots, branches, and leaves is less visible (moreover, Filatov has pointed out that wisent "nibble" shoots of trees the thickness of the little finger). They avidly consumed the bark of elm and mountain ash, followed by hornbeam, pine, willow, sycamore, high-mountain maple, aspen, fir, yew, and others (Bashkirov, 1939; and others). In spring wisent often gnawed at the bark of pear and apple trees (Pfizenmayer, 1929). Wisent peeled the bark of standing trees in strips measuring 2.0 to 3.0 m (mainly in spring) or gnawed it from fallen tree trunks. Wandering in the snow, they plucked at the coarse leaves of holly and often dug up with their hooves long vines of blackberry, and later all their stalks and green leaves. At places where the snow was less they consumed twigs, and mountain fescue, which remains green in winter. Mistletoe was well liked year-round and arboreal lichens eaten in winter (*Usnea*).

Observations on wisent living now in Caucasian preserve reveal that in pens and under semifree conditions they eat (according to data of 1955) 240 varieties of plants, including 209 herbaceous plants, 26 trees and shrubs, 2 types of ferns, and 3 varieties of lichens.

---

[44] Present-day wisent of Caucasian preserve very rarely nibble ferns (Krainova, 1951).

[45] In Priok-Terras preserve wisent similarly gnaw at the roots of elms (Zablotskii, 1957) and in Caucasian preserve at the roots of a whole series of trees (Aleksandrov, 1958).

[46] Present-day wisent of Caucasian preserve consume acorns but only a small quantity (Krainova, 1951).

Foremost among the herbaceous foods are grasses (of these 80% represent the main favorite foods, especially orchard grass, false brome grass, timothy, etc.). Forb species serve as secondary and occasional food and represent only 20% of the main diet (cow parsnip, goat's-rue, and others). From among tree and shrubs, elm, aspen, goat willow, hornbeam, *Euonymus,* hazel nut, pear, etc. are preferred. Mountain fescue and forest sedge, which remain green in winter, twiggy food of different varieties, arboreal lichens, *Euonymus,* aspen, elm, blackberry, and others are important in winter. Grasses are of particular importance in the diet of wisent in April and May. Herbage is used selectively; often only some individual plant parts are consumed. The daily norm of herbaceous food for adult wisent is 30 to 45 kg, on the average 36 kg, calculated as green weight (Aleksandrov, 1958; Kalugin, 1958).[47]

In Belovezh Forest in the past wisent consumed in summer mainly herbaceous vegetation and more rarely browse. In the stomach contents of ten wisent the latter constituted 20% of the summer mass (mostly bark of aspen and ash) versus 80% grass. Preference was shown for the freshest and most succulent grass; they also consumed in summer small branches of trees, bilberry stalks, and mushrooms (chanterelle and honey agaric) (Vrublevskii, 1912, and Wroblewski, 1927). From among herbaceous vegetation, wisent avidly consumed in summer grasses, especially alpine sweet grass, foxtail, timothy, wood millet, mint, fescue, and others; as fall approached shoots of deciduous trees were more often consumed. In autumn fallen leaves of aspen, ash, and maple were eaten avidly (Kartsov, 1903).

In winter Belovezh wisent fed on hay (with extreme discrimination), twiggy food, thin branches and bark of ash, aspen, willow, and other trees and shrubs, arboreal lichens,[48] heather (the latter was almost totally destroyed by ungulates in the forest by the end of the first decade of the twentieth century), bilberry stalks, mistletoe, and others (Dalmatov, 1849; Kartsov, 1903; Kulagin, 1919; Vrublevskii, 1927).

According to Wroblewski (1927), tree browse was occasional summer food and a compulsory winter food for wisent; on the whole, however, wisent are grazers. These observations run counter
406 to the actual data of that period[49] and to observations made in other

---

[47] See Krainova (1951) for the food of wisent in Caucasian preserve based on observations from 1942 to 1946.

[48] Kartsov used the popular name "moss"; the same error was repeated by Kulagin (1919) and Serzhanin (1955).

[49] In all probability Wroblewski attributed the foliage of trees and shrubs to the graminaceous category.

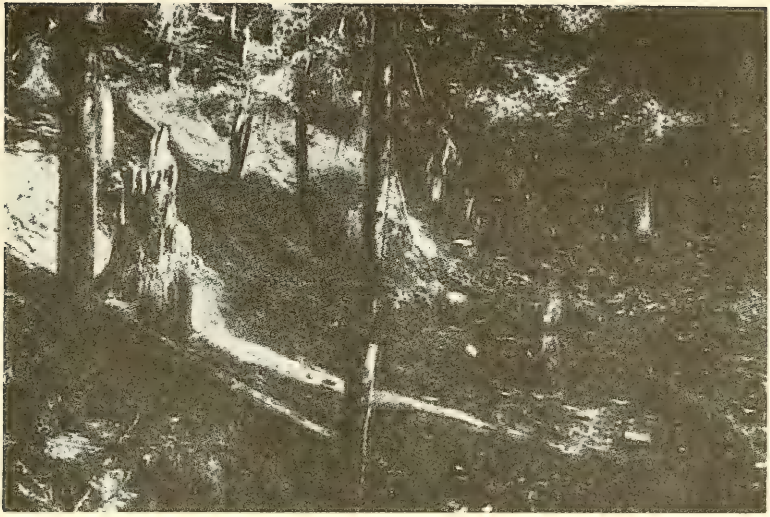


Fig. 128. Largest natural salt lick, Mamaev (Pshekish, Caucasian preserve), which was well visited in the past by wisent and is often visited now by deer. September, 1937. Photograph by A.A. Nasimovich.

regions, including the most recent. Wisent consume browse food avidly year-round,[50] mainly in the form of leaves in summer (Zablotskii, 1957). Observations made on wisent in Belovezh Forest preserve have established that in pens and under semifree conditions these animals avidly consume no less than 170 species of herbaceous plants and 17 varieties of trees and shrubs, including acorns (Zablotskii, 1957).

In Priok-Terras preserve present-day wisent grazing outside pens consume no less than 109 species of herbaceous plants and 32 species of trees and shrubs; the corresponding numbers in pens are 150 and 25 species. At the end of May the leaves of trees and shrubs are consumed in large quantities and serve as the main food. Tree browse, mainly leaves, comprises no less than 50% of the entire intake of wisent on summer days. From among herbaceous plants, fibrous sedge, willow herb, golden-rod, lily-of-the-valley (in pine forest, at grazing places, an average of 80% of all lily-of-the-valley plants are consumed), saltwort, etc. are consumed particularly often in the snowfree period. The tops of tender reed stalks are well liked. Mushrooms—chanterelle, white mushroom, birch mushroom, and others—are consumed relatively often[51]; fruits of bird cherry and mountain ash are also consumed. Wisent tear off tree bark at temperatures not below –15°C (Zablotskii, 1957).

---

[50] Ya. Zhabinskii was one of the first to notice this in relation to European wisent (Zablotskii, 1949).

On the whole, in all the three main regions in which wisent are present in the Soviet Union, no less than 400 plant species, including over 50 tree and shrub, are consumed. From among herbaceous plants, those most preferred are large succulent grasses growing in places of high and moderate humidity (Zablotskii, 1957). Even 407 primeval wisent could be considered more adaptable in food selection than is apparent from the few stray observations passed on to us by earlier zoologists.

It is known that wisent of the western Caucasus visited natural aquatic salt licks, especially in spring; they visited some even in winter (Nasimovich, 1938). They also visited artificial salt licks but less often than deer (Kartsov, 1903). It has been noted several times that wisent raised in Caucasian preserve eat soil (Krainova, 1951).

Home range. In Belovezh Forest small herds of females with young were confined in the past for much of the summer to a single region and undertook minor migrations into different types of habitats within it (Kartsov, 1903; Wroblewski, 1927). In winter, when food supplements were given, the herds roamed from one shed of hay to another, often covering areas of 500 to 600 hectares (Kartsov, 1903).

In the period of rut wisent, especially adult males in search of females, wandered extensively. Filatov (1910) tracked wisent in the Caucasus in that period (August to early September) and sometimes had to follow a fresh track of unfrightened animals for 3 to 5 hrs (probably corresponding to 5.0 to 7.0 km) before he could catch up to them. In early September a herd consisting of four or five wisent lived in a small section in a forest glade for about two days after traveling 6.0 km. Had the animals been frightened, they would have moved away into an altogether different place (Filatov, 1910). Wisent tracks to salt licks covered several kilometers; a large number of animals (Dinnik, 1897), evidently from different sections of the region, visited salt licks. In winter, especially in the period of abundant snow, wisent lived for long periods in a single region without undertaking noticeable migrations.

In Priok-Terras preserve today free-ranging wisent wander most extensively (up to 4.0 to 5.0 km a day) in the second half of May and the first half of June. Under conditions of free grazing (with food supplements in winter) the herd is confined to a region of 500 to 1,000 hectares (Zablotskii, 1957). In summer wisent in Caucasian preserve traverse daily 1.5 to 3.0 km and often 10 to 15 km in autumn (almost nonstop; Kalugin, 1958).

---

[51] In Caucasian preserve the intake of arboreal bracket fungi has also been noted (Aleksandrov, 1958).

Daily activity and behavior. In summer wisent used to graze mainly in the morning and evening and perhaps also for part of the night;[52] on warm days they moved into the forest for shelter to ruminate. In the Caucasus they set out to graze in low alpine meadows and glades and hid in beds in the forest; in heavy rains they settled under large fir and spruce trees. On cold days the animals grazed during the daytime also, sometimes directly in the forest; on warm days, they lay down or stood mostly in the same place, visiting the grazing ground or water source three to four hours before sunset. A bed was often made in porous soil under fir trees (Dinnik, 1910; and others).

In the mountains of the western Caucasus wisent usually visited *solonetzes* [salty soil] early in the morning and evening. Bison were never known to bathe (Wroblewski, 1927).

Recent observations on freely grazing wisent herds in Caucasian preserve revealed that they rest for about 17 hrs a day in summer and 15.5 to 18 hrs in winter. Wisent spend maximum time grazing in winter and spring—in spring up to 10 hrs and in summer 5 hrs a day. In the warm period of the year they visit water sources not less than twice a day; they ignore the water source for two or three days during rains. The maximum daily water intake may be as much as 50 liters (Kalugin, 1958).

Wisent often roll on dry porous soil and sand and visit such places regularly. They do not wallow in mud or marshy places (Wroblewski, 1927; and others). In moving through snow they plough in deeply. When the snow cover is deep, animals in a herd move without deviating from the tracks of others, forming a regular corridor through it. Having sensed food under shallow snow (20 to 30 cm), wisent dig a pit with their muzzle by rotating the head.
408 Hooves are rarely used and the animals never dig in deep snow[53] (Filatov, 1910; and others).

When necessary, wisent can run fast on snow of up to a meter in depth, usually in a gallop. They do not gallop for more than 400 to 500 m. They can easily clear a 3.0 m ditch or a 2.0 m high fence

---

[52] According to Wroblewski (1927) wisent in the forest grazed throughout the night.

[53] According to Krainova (1951) wisent of Caucasian preserve often rake the snow first with the hooves and then widen the pit with the muzzle, thus reaching food. Steppe bison also behave in a similar manner (McHugh, 1958).

(Kartsov, 1903; Wroblewski, 1927). Caucasian wisent freely negotiate very steep places and avoid only rocks. When frightened, they run in a cohesive group, usually down the slope (Dinnik, 1910; and others).

In his first observations on wisent in the Caucasus, Filatov was most amazed at the agility of their movements. Wisent "moved from place to place, tore coltsfoot, turned, and now and then raised their head and listened. The animals performed all this in an extremely rapid tempo and very easily. There is nothing cumbersome or lazy about them as in the case of domestic cattle . . . . Let the wind blow toward it and the animal disappears instantly in long jumps without even turning toward an intruder" (Filatov, 1910). The next day Filatov happened to observe the same wisent eating blackberries. "The wisent scurried backward and forward as rapidly as on the previous day but hid behind a tree, coming out into the open periodically. On sighting an exposed root, it knelt and gnawed at it while on its knees" (Filatov, 1910).

Olfactory and auditory senses are well developed in wisent but they mostly rely on their sense of smell. Vision is comparatively weak. On noticing a man, Caucasian wisent usually hid instantly and females generally gathered their calves. In rare cases the animals adopted a menacing posture—lowering the head, puffing, assuming an air of combat, and later retreating. Actual attacks on man have been observed occasionally (Dinnik, 1910). In Belovezh Forest instances of wisent attacks on man were apparently more common. More often it was the female which attacked to protect her calves; lone bulls, especially in the period of rut, also attack (Kartsov, 1903; Wroblewski, 1927). The young are inclined to be "playful". Calves often chase each other, butt each other, and so on.

Most wisent lived in herds years ago. In the Caucasus adult females with calves and animals of both sexes up to two or three years of age moved in groups of six to eight, more rarely of ten to fifteen animals. Adult males generally remained isolated but also appeared in groups of smaller sizes (three or four animals). Herds of 20 to 30 animals were evidently chance groupings and observed most often at salt licks (Bashkirov, 1939; and others). In Belovezh Forest herds were usually no larger than 15 to 18 animals, quite often less, and old males often moved singly. Kartsov (1903) recalls that "formerly" wisent herds were 40 to 50 strong; this, however, is dubious. The gregarious tendency was more pronounced in winter (Kartsov, 1903; Dinnik, 1910) and in the period of rut. In hours of mass flight of horseflies wisent in the forest sometimes formed groups of up to 30 to 50 animals which later split up (Wroblewski, 1927). Old males remained in herds of females only during the period of rut or a little longer.[54] According to Wroblewski (1927) some males spent the period of rut in the same herd of females year after year. Herds of males split up in the period of rut.

In relatively large herds of wisent consisting of several adult females, calves, and animals of both sexes up to two or three years of age, hierarchic relations were distinct (Kartsov, 1903); a single adult female was given access to food first. Such animals were usually called leaders. Krainova (1947) has observed a similar behavior among wisent of Caucasian preserve.

409 Kartsov (1903), Filatov (1910), and Wroblewski (1927) regarded a herd of wisent, based on its composition, as a large growing "family." This has not, however, been confirmed by actual data and is evidently not true. Exhaustive studies on [American] bison have shown that, in spite of prevailing views, herding is not usually based on characters of "relationship", and a herd should not be considered a large growing family. "Familial relations" usually bind only females and their calves, extending in some cases to yearlings (McHugh, 1958).

Seasonal migrations and transgressions. Wisent of Belovezh Forest undertook only local migrations in the past, in the course of which they moved from one habitat to another (see the section "Habitat"). In the western Caucasus seasonal migrations were distinct. In spring the animals climbed high into the mountains, descending into the lower part of the boreal forest belt in autumn; in the remote past, they descended even into broad-leaved forests where there was less snow. The spatial magnitude of migrations ranged from 10 to 30 km; it was even extensive in the nineteenth century.

Spring migrations were very gradual and commenced in April. In autumn some herds remained a long time in places of their summer residence and sometimes moved downward even after the formation of a thick snow cover. Some wisent gathered for wintering in elongated valleys with relatively little snow (Zakhan, Umpyrka, and Achipsta) at the center of the montane region. Some animals wintered deep in the mountains (Kholodnaya and Kitaiskaya Rivers), spending much of the season in an extremely restricted territory (Filatov, 1910 and 1912).

Vertical seasonal migrations of Caucasian wisent were necessitated by a series of factors (food availability, dispersal of snow cover, degree of abundance of blood-sucking flies in different sections of

---

[54] In analogous instances in bison old females commanded the "leadership" position in the herd (McHugh, 1958). A similar phenomenon was also recorded among wisent (Kartsov, 1903).

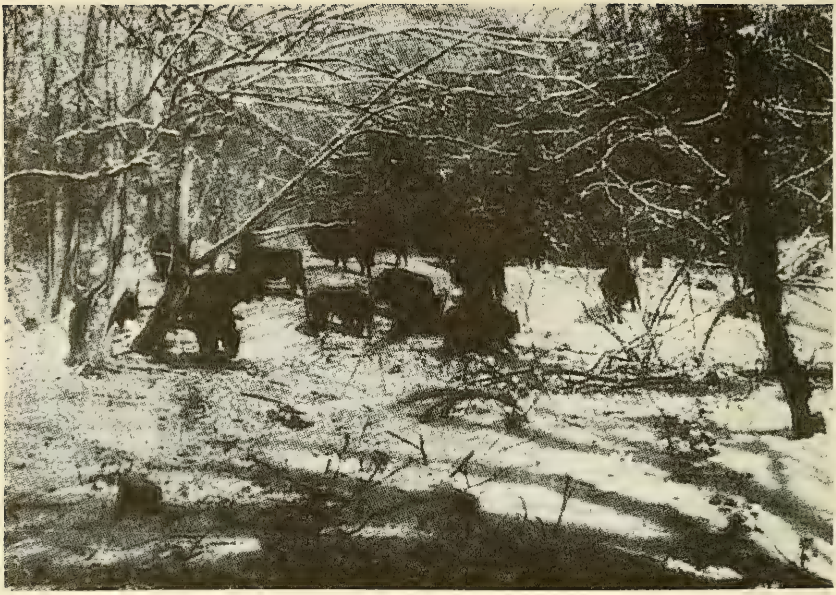


Fig. 129. Wisent in winter in the Kishi basin. Caucasus preserve. February, 1955. Photograph by V.N. Aleksandrov.

the locality, human factors, etc.). This should not be explained as caused exclusively by their search for habitations with vegetation in their early growth phases (Zablotskii, 1957).

When wisent in Caucasian preserve were recently placed in free-living conditions, they also began performing regular seasonal 410 migrations—in winter downward along the mountain slopes and in summer up into the mountains. The range of these migrations has risen perceptibly over the years. Migrations are very pronounced among the Umpyrka herd of wisent living in the mountains. Kishi wisent in recent years have been sighted more often in the lower mountain belt, north of the preserve boundary (Novoprokhladnoe village); some males have reached Abadzekhov station situated in the foothills (S.G. Kalugin).

In Belovezh Forest and especially in the western Caucasus instances of wisent intrusions into regions situated several dozen kilometers away from places of their permanent residence have been recorded several times. In the western Caucasus such transgressions were observed as long as wisent survived there and their frequency increased in their last few years (Bashkirov, 1939). In 1915 a wisent was killed 15 km away from Sukhumi (Pfizenmayer, 1929), no less than 100 km from the nearest point of its permanent habitation.

These intrusions were probably associated with constant persecution by man and with males in search of females during the period of rut.

Reproduction. Belovezh and Caucasian wisent came into rut roughly around the same period in the past, during August and the first half of September. According to Dalmatov (1849) and Kartsov (1903), Belovezh Forest wisent came into rut usually from the end of July through early September of the old calendar, corresponding roughly from August 10 through September 15 of the new calendar. Estrus in some females continued for about two weeks (Kartsov, 1903) or for six to eight days (Kalugin, 1919). The duration of rut varied in different years (Karstov, 1903).

According to Dinnik (1910) Caucasian wisent came into rut in August and probably also in the first half of September of the old calendar (from August 15 through September 15 to 25 of the new calendar). According to Vinogradov (1872) Caucasian wisent were in rut from August of the old calendar, with rut generally continuing for about three weeks. According to Filatov (1910) rut in Caucasian wisent occurred in "August" (August 15 to September 15 of the new calendar). These data should have been more accurately ascertained. Dinnik (1910) recalls that in a sample of young wisent from April 27 (May 11) through May 8 (May 22) more than ten extremely small or even newborn calves were found; of these, six were captured on the very first day of the hunt. The gestation period of wisent was close to nine months. Among wisent raised in Caucasian preserve now it varies from 261 to 283 days[55] (Kalugin, 1958). This means that females which calve from May 11 through 22 or a few days earlier should have mated between August 1 to September 5.

In the period of rut adult males generally not less than six or seven years old, often even older, attached themselves to a herd of females and calves and juveniles of both sexes. With the appearance of a male in the prime of life in the herd, bulls older than two years were driven out (Wroblewski, 1927). Calves and yearlings remained with the herd. In the Caucasus in the period of rut such a herd comprised two to six mature females forming a harem (Radde, 1899). During rut adult animals were excitable and less cautious. Bulls often stamped the ground with their hooves, stripped bark from branches of tender (up to 10 to 12 cm diameter) trees with their horns, and sometimes uprooted them or broke them. Often males were seen in a threatening posture and emitted hoarse rumbling sounds. Several investigators (Kartsov, 1903; Bashkirov, 1939; and others) point out that in the period of rut wisent exuded an odor resembling that of musk, which was quite strong in males. Males ate little (the stomachs of killed animals were usually empty) and became highly emaciated during this period (Dinnik, 1910).

---

[55] According to Zablotskii (1957) gestation lasts 262 to 267 days.

Between adult wisent, including females, combats were frequent, but genuine fights between males for females were not. The latter were usually limited to demonstrations, during which the weaker bull preferred to retire immediately or after the very first clash of foreheads without a close fight. Yet bitter duels were also observed in
411 which the bulls clashed foreheads for quite some time, until the opportunity came to strike the rival on the side with the horns and inflict severe injuries or even kill him (Kartsov, 1903; Wroblewski, 1927; and others).

Due to the availability of winter food supplements in the Forest and year-round in pens for captive wisent, the period of rut of Belovezh animals gradually shifted from the former period August–September. While Kartsov (1903) considered instances of mating outside the normal period, for example in December, as relatively rare deviations, such instances were notably more frequent a decade later, especially among animals held in pens (Wroblewski, 1927). The prolonged period of rut among Belovezh wisent also attracted the attention of Kalugin (1919). A similar phenomenon was observed among Askaniya wisent (Zablotskii, 1940). It is even now seen among wisent raised in Caucasian preserve (Kalugin, 1958) and in other regions of the USSR (Zablotskii, 1949 and 1957).

The most common period of calving of wisent in the western Caucasus and in the old Forest was from May 5 to 10[56] through June 15.[57] In the Forest in the early twentieth century, calving as well as rut were more protracted; calving occurred from May through November (Kalugin, 1919). Young females calved at a place away from the herd and remained aloof for five or six days. Older females often returned to the fold immediately since calving occurred close to the herd (Filatov, 1910). Dinnik (1910) recalls that while catching calves on May 11 in a section of about 50 hectares, three females with very young calves were found at different spots. It is almost certain that these animals belonged to the same herd. Calved females immediately ate the placenta (Wroblewski, 1927), a fact subsequently confirmed in observations on bison raised in pens (Zablotskii, 1957).

Usually only one calf was born. Instances of twins in the Caucasus were extremely rare (Pfizenmayer, 1929) but evidently more frequent in Belovezh Forest (Wroblewski, 1927). Most females did not calve annually but perhaps once in two years. In the Forest this was assessed from observations of wild and captive animals (Kartsov, 1903; and others) and in the Caucasus based on indirect evidence, i.e., low numbers of wisent with calves in their first year in the herd (Dinnik, 1910; Filatov, 1910). Biennial calving was explained as due to prolonged lactation (Wroblewski,1927), which is not correct, and due to lack of food (Kartsov, 1903), which perhaps is more correct. Most wisent when raised and fed well bear calves every year (Zablotskii, 1957).

---

[56] According to Dinnik (1910) and Pfizenmayer (1929), calving mostly occurred at the end of April (old calendar) but generally continued for 1.5 months.

[57] All the dates given here and subsequently are according to the new calendar.

In pens and under semifree conditions sexual maturity of males sets in at the age of two or three years, and in the second year itself very rarely. In Caucasian preserve one instance has been recorded of a 16-month-old bull mating with a female which calved. Females become mature in the second year but some mate only in the third year[58] (Zablotskii, 1949 and 1957). Under natural conditions bulls younger than six or seven years could not successfully withstand competition from older males and mated only occasionally. Older females came into estrus earlier than young ones (Kartsov, 1903). Data about females attaining sexual maturity at the age of five or six years (Kartsov, 1903; Kalugin, 1919; Severtsov, 1940; and others) appear erroneous.

Growth, development, and molt. An hour after birth the calf stands on its legs, unsteadily at first and with increasing confidence later. After another 30 minutes or so it can follow its mother with a stumbling and unsteady gait (Zablotskii, 1957). Under natural conditions calves remain at one place for the first few days, the female staying closeby. After about a week, or earlier, calves follow their mother everywhere. By then they usually join the herd (Kartsov, 1903; Wroblewski, 1927).

412 According to Kartsov (1903) females calving early ceased suckling when the calf was five months old. Calves born later suckled up to a year and sometimes even longer. Calves 1.5 years old had to go down on their knees to get at the udder. Females with a newborn calf usually drove away their older offspring, but instances of their continuing to suckle have been noted (Wroblewski, 1927). Calves began eating grass at the age of 19 to 22 days (Krainova, 1951). Horns commenced growth from the first autumn of life (Kartsov, 1903). Calves remained with their mother up to a year or two.

---

[58] The periods of sexual maturity of male and female [American] bison correspond roughly to those given above for wisent (McHugh, 1958).

A newborn calf weighs 22 to 23 kg (M.A. Zablotskii). An adult Belovezh female wisent weighed roughly a third less than the male of the same age (Kartsov, 1903). Belovezh wisent were larger than Caucasian animals; males weighing 800 to 850 kg were evidently not rare and some bulls weighed even a [metric] ton. Evidently much larger animals were more frequently encountered during the twelfth to the sixteenth century (Tsalkin, 1951). The weight of Caucasian male wisent usually did not exceed 750 to 800 kg but much larger animals were not uncommon (Bashkirov, 1939). A hybrid wisent-bison, "Ermysh" (51/64 wisent), in Caucasian preserve weighed 1,150 kg (S.G. Kalugin), probably a phenomenon of heterosis.

According to observations made in nurseries the maximum longevity of males is 22 years and of females 27 years. One female lived to age 26 years and calved regularly at the age of 21 to 24 years[59] (Zablotskii, 1957). Wroblewski (1927) thought that Belovezh wisent survived for not more than 35 years; the teeth of old animals were totally worn away and they were unable to masticate food properly. The assumption of Kartsov (1903) that bison lived up to 50 years of age is incorrect.

Wisent were characterized by a single molt, in spring, during the year. Among Belovezh wisent molt commenced at the end of February or in March, being earliest in better fed animals. The shedding of winter hair commenced from the neck, head, and legs, followed by the chest, sides, and back. The mane was also sloughed. The last shedding occurred at the rear of the trunk. Among adult animals molt continued uniformly without the formation of bald patches. In May the mane began to grow perceptibly. At the end of July, i.e., toward the commencement of the period of rut, the animals were in full summer coat and sported short hair without underfur. Sometimes bunches of winter wool were left behind only on the sacrum. From August guard hair commenced lengthening and underfur became visible. By October hair growth reached the winter level and the coat darkened markedly (Wroblewski, 1927; and others).

Judging from the descriptions of Dinnik (1910) and Filatov (1910) molt of Caucasian wisent occurred later than in Belovezh wisent[60] and proceeded roughly as follows. In mid-May molt was almost imperceptible at a distance and the animals preserved the long winter guard hair and much of the mane. Shedding of guard hair intensified only in the first ten days of June and then molt advanced rapidly. Nevertheless, even at the very end of June a herd was observed in which all of the females at a distance appeared to be in winter coat. Much of the winter hair was also seen on wisent encountered on July 22. Yet, even in the latter half of June adult males with a transitional coat were sometimes sighted, with very sparse hair or none and almost no mane. At the end of September the growth of wool was at its peak; it was fairly long until this time only on the head.

---

[59] Observations in the USA of marked bison revealed that females older than 30 years sometimes bore calves. Among females aged 25 to 35 years old, 21% were pregnant (McHugh, 1958).

[60] According to Kalugin (1958) wisent of Caucasian preserve molted from the latter half of February (males) to the end of March (females). Molt ceased from May (males) to July (females).

Enemies, diseases, parasites, mortality, competitors, and population dynamics. Even large predators pose a danger mainly for young wisent; instances of successful wolf attacks on adults are relatively rare (Kartsov, 1903; Bashkirov, 1939). In the Caucasus calves might fall prey to the leopard but this has not been confirmed by actual observations. Pfizenmayer (1929) reports finding wisent calf rem-
413 nants in the stomachs of bear. It is almost certain that these bear must have eaten dead calves since Caucasian bear are not known to be predators (Nasimovich, 1940). Lynx is usually listed among the potential enemies of calves.

Snowy winters, quite frequent in the Caucasus, were difficult even for adult wisent since they had been driven away by man from their most convenient wintering sites and many animals were emaciated by spring (Filatov, 1910). Carcasses of dead animals were found after the snowy winters of 1907 and 1908 (Dinnik, 1909 and 1910). Analogous reports exist for the spring of 1920 (Bashkirov, 1929). However, wisent withstood well the extremely snowy winter of 1910 to 1911 (Filatov, 1912).

Among the factors responsible for wisent mortality perhaps the most important are infectious epizootic diseases, to which many references exist. Helminthiasis is similarly fatal to wisent. Hoof-and-mouth disease and pasturellosis are evidently extremely serious. To a lesser extent emphysematous carbuncle, general inflammation of the lungs (pleuropneumonia), and possibly Siberian ulcers are also responsible for wisent mortality. In Belovezh Forest instances of death due to trypanosomiasis or "sleeping sickness of wisent", caused by *Tripanosoma wroblewski,* have been noted (Vrublewskii, 1908 and Wroblewski, 1927). Wisent suffer from tuberculosis, brucellosis, various intestinal disorders (extremely widespread in Askaniya-Nova), tetanus, rabies, actinomycosis, and probably also from piroplasmosis, but their incidence under natural conditions was insignificant, compared with hoof-and-mouth disease, pasteurellosis, and some other diseases.

Epizootic hoof-and-mouth disease was reported among cattle of western Caucasus in the 1890's and in 1907 and 1919 (on the latter occasion, Siberian ulcers were also reported). These diseases also killed wisent (Dinnik, 1909; Bashkirov, 1939). It is possible that in 1919 and 1920 dead Caucasian wisent included those killed by emphysematous carbuncle, which affected cattle at that time (S.A. Severtsov, 1926). In 1910 and 1911 over 50 wisent died in Belovezh Forest due to epizootic pasteurellosis[61] (Eckhardt [?] and Fedders, 1912*; Wroblewski, 1927).

Wroblewski (1927) performed an autopsy on 88 wisent dead or killed under different circumstances mainly during 1907 and 1908. Of them, 40 had died from diseases including helminthiasis, 11 had been killed by wisent themselves (2 adults and 9 calves; the latter were killed and left by adults mostly near haystacks), 8 had died of old age,[62] 2 had drowned, and 11 died due to limb fractures, "pneumonia" (resulting from the entry of foreign bodies into the respiratory tract), intake of deleterious matter, etc. Mortality was highest in winter and spring, especially in March and April. Among those killed by diseases, including helminthiasis, 13 (roughly one-third of the total) died from distomatosis ("fascioliasis") caused by liver fluke. In one wisent 668 mature flukes were counted in a third of the liver. Of all the wisent examined, flukes were absent only in 3 calves; 9 wisent had died from a general inflammation of the lungs, 5 from trypanosomiasis, 4 from emphysematous carbuncle, etc. (Wroblewski, 1927).

In 1904 an epizootic disease raged in the Forest and killed 172 wisent; judging from the symptoms, Wroblewski thought that it was almost certainly emphysematous carbuncle. In the Forest wisent suffering from hoof-and-mouth disease were seen every year; quite often the animals died as a result of various complications and general emaciation (Wroblewski, 1927). Some undiagnosed epizootic diseases affected the wisent of Belovezh Forest in the nineteenth century (Kartsov, 1903; and others).

Wisent harbor about 20 species of helminths (3 species of trematodes, 4 of cestodes, and 13 of nematodes) (Belyaeva, 1958). The most pathogenic are liver flukes and pulmonary strongylids [lungworms]. According to Kalugin (1919) instances of death due to distomatosis ("fascioliasis") were more frequent following a rainy summer. In the Caucasus wisent did not suffer from distomatosis since there are
414 practically no intermediate hosts for flukes, i.e., aquatic mollusks,

---

[61] S.A. Severtsov's (1933) data that 60% of the wisent population, i.e., several hundred animals, died as a result of this epizootic disease are incorrect.

*Not in Literature Cited—Sci. Ed.

[62] Instances of death of wisent due to old age have also been reported by Kartsov (1903). Filatov (1910) killed a Caucasian wisent which had teeth worn down to the gums.

there. In Askaniya-Nova wisent suffered from echinococcosis (Zablotskii, 1939); many suffered from diseases caused by the nematode *Thelazia rhodesi,* which resulted in corneal opacity and sometimes blindness (Rukhlyadev, 1939). Helminths parasitizing Caucasian wisent have remained almost univestigated to date. Filatov (1910) found no parasites in the wisent dissected by him.

Larvae of skin and nasopharyngeal gadflies were not detected in animals dissected in the Forest (Wroblewski, 1927). Bison were parasitized by the deerfly *Lipoptena cervi,* ixodid ticks, and other mites (Rukhlyadev, 1941). Instances are known of wisent in zoological parks falling sick from psoroptic mange (Dubinin, 1955).

Fairly frequent combats between wisent often resulted in severe injuries and sometimes even death. Wroblewski (1927) dissected many wisent which had died for various reasons; some revealed healed rib fractures and other traces of injuries. Instances are known of heavy old males breaking the backs of females in attempting to mate. In Belovezh Forest and the Caucasus newborn calves often died, but the reasons for their mortality remain vague. According to S.A. Severtsov (1940), about 50% of calves born died in their first year.

At birth the ratio of the sexes among calves was close to 1:1 (Zablotskii, 1957). Among 125 calves born in Caucasian preserve from 1942 to 1955 males constituted 52.8% and females 47.2% (Kalugin, 1958).

According to a count made in March, 1909 the wisent population in Belovezh Forest comprised:[63]

Males above 3 years	256	36.8%
Females above 3 years	329	47.3%
Calves of 1 to 2 years	111	15.9%
Total	696	100%

Counts made in January, 1914 gave the following results:

Males over 3 years	231	31.8%
Females over 3 years	347	47.7%
Calves of 1 to 2 years	149	20.5%
Total	727	100%

Among adult wisent, males in the first of the above two counts constituted 43.8% and females 56.2%; the corresponding figures in the second count were 40% and 60%. Consequently, mortality of males was slightly higher[64] than that of females; nevertheless, considering the polygamy of wisent, there were sufficient males in a herd to intensify intraspecific competition.

---

[63] Including some wisent in pens. The numerical counts are from Wroblewski (1927).

An analysis of statistical quantitative counts of wisent in Belovezh Forest over many years revealed that increase in herd size was rather negligible (S.A. Severtsov, 1940; Zablotskii, 1957).

Red deer, imported in the mid-1860's and later proliferating very well, were of great importance among competing species in Belovezh Forest. In 1908 deer numbered 4,769 in the forest (Wroblewski, 1912) and continued to multiply in subsequent years. Deer suppressed, and at places almost totally destroyed, the underforest and the growth of deciduous trees, thereby impoverishing the tree and shrub foods available in the forest. Vrublevskii/Wroblewski (1912 and 1927) has attributed the low build up in wisent population mainly to unfavorable competitive relations with deer.

415 Fallow deer intensely consume arboreal food, as observed quite early by Kartsov (1903), and hence could be regarded as a fairly important competitor of wisent. In the first decade of the forest there were about 2,000 fallow deer (Vrublevskii, 1912). Roe deer were even more numerous but their role as competitors of wisent was considered less serious. Elk in the forest were very rare. Competition with other species of wild ungulates and wisent in the western Caucasus did not exist. According to Filatov (1910) wild boar used the tracks of wisent in moving through deep snow.

Cattle are subject to the same diseases as wisent and promote the spread of various epizootic diseases among them. The spread of fascioliasis among wisent in the Forest was associated with the presence of feral sheep suffering from this disease (Bashkirov, 1939).

Field characteristics. In external appearance wisent differ distinctly from other animals and no confusion is possible. Males are much larger than females, their horns thicker with the ends less closely disposed, and hump larger than that of females (in young wisent the hump is almost indistinct).

In the first years after the extinction of wisent in the western Caucasus, when the local population came to know about the search for these animals, tracks of domestic [water] buffalo and large ox were often mistaken for those of wisent. According to a description by Kartsov (1903) the hoofprint of a wisent, though similar to that of a cow, is far deeper and larger. Even the print of a young wisent is larger than that of a medium-sized bull. That of a female is more oblong

---

[64] During hunts males were mainly shot, but in recent years hunting of wisent has been banned and it is far easier for poachers to kill a female than a male.

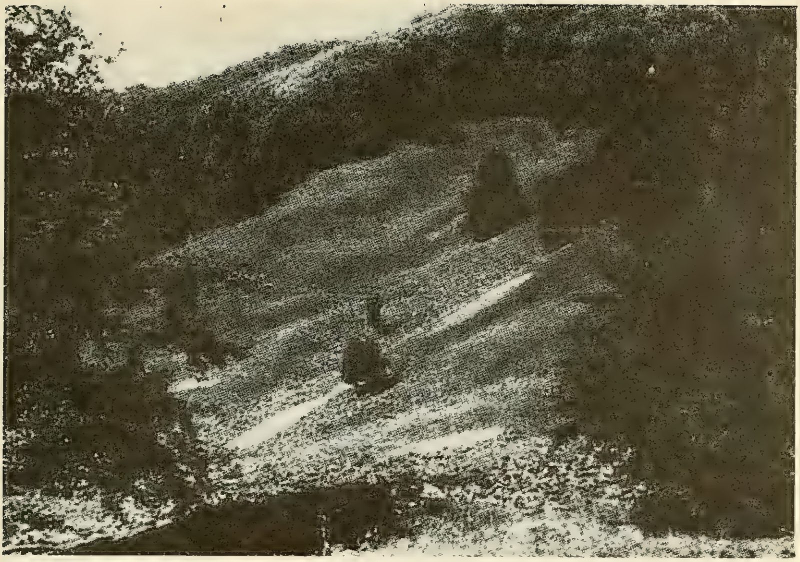


Fig. 130. Areas where wisent lie and roll on the ground. Temnaya Polyana. Caucasian preserve. August, 1954. Photograph by V.N. Aleksandrov.

than that of a male. The normal pace of Belovezh wisent is 75 to 115 cm, during canter 130 to 155 cm, and in gallop 170 to 200 cm. Frightened wisent can jump up to 3.0 m. In galloping the hoof impressions of the rear legs come in front of those of the forelegs by 20 to 25 cm. Hoofprints of running animals are deeper than those of animals moving at an even pace; in the former case impressions of the tiny lateral hooves are visible in mud. In running the hooves spread wider than in walking. In moving on a sticky substrate such as mud or snow the animal lifts the hind legs from the cup-shaped pit directly upward with almost no drag (drag is invariably seen in cattle). At places of regular migrations of wisent well-beaten trails form (Kartsov, 1903; Wroblewski, 1927). The hoof length of the forelegs in adult wisent is 7.0 to 10.5 cm and of the hind legs 7.5 to 11.5 cm (Flerov, 1932). Hoof-print impressions are slightly larger than the hoof
416 dimensions. Wisent feces resemble those of cow but the latter's are more fluid in consistency (Wroblewski, 1927).

In places of permanent residence of wisent are small areas (up to 100 m^2), and sometimes even pits with loose soil, in which the animals roll and lie down. Wisent often use the same trees for scratching and polish their bark, leaving behind hair, especially the underwool. Young trees, in cross section up to 10 to 12 cm, are often broken or uprooted as a result of being constantly swayed by the horns. In areas of pasturage grazed spots are distinct and broad incisions visible on the bark of trees; the bark of deciduous trees is often stripped up to 3.0 to 4.0 m above the ground. At places of wisent skirmishes the ground is ploughed over an area of 10 to 20 m^2 and small trees broken.

The voice of wisent is rarely heard. A sort of jerky low grunt issues from adult animals, irritated animals rumble, frightened animals snort, and wounded animals sometimes bellow (Filatov, 1912). (A.N.)

Economic Importance

In the mid-1800's the meat of wisent was a notable supplement for peoples of Karachaev-Cherkessy regions. According to Vinogradov (1870), who traveled in 1868 into the mountains of northwestern Caucasus, in the recent past "Russian military contingents found a huge amount of wisent meat prepared in various manners in the villages in the mountain belt" (p. 185).

According to Dinnik (1910) wisent meat is tough with coarse fibers but satisfactory in taste. According to Wroblewski (1927) wisent meat hardly differs from that of cattle, only the meat of older animals being tough (most chroniclers tasted only this type) and the meat of young wisent is excellent. Large bulls used to yield up to half-a-ton of meat.

The hide is strong and very thick but porous. Furriers valued it (Bashkirov, 1939). People used it in harnesses and other belt-like articles. The back portion of the hide was particularly valued because it was the toughest. Poachers in the mountains often took away only the back portion of the hide (a whole hide weighed about a centner [= 100 kilogram]) and some meat, leaving the rest to rot (G.I. Bessonnyi).

In the past in the western Trans-Caucasus goblets made from wisent horns and ornamented with silver were greatly valued at banquets (Nordmann, 1838).

The milk of wisent is very fatty (Wroblewski, 1927).

Wisent were hunted from ambush, waylaid at salt licks, and in the Forest, driven up by hunters. Wisent, especially the male, were difficult to down with a single shot, given the type of guns available then, and hence many injured animals escaped. Old bullets were recovered from the carcasses of a few animals caught later.

Hybridization experiments of wisent with cattle[65] have been conducted for more than a century—and with [American] bison, commencing in the first decade of the nineteenth century in Askaniya-Nova. Hybrids are characterized by large size, similar to hybrids of draft animals, and capable of hard work.

---

[65] Wisent have been crossed with Swiss animals, and more recently also with Ukrainian gray, and other breeds of cattle.

In the past instances have been recorded of damage to oats and winter and kitchen gardens (wisent will dig up potatoes, beets, and Jerusalem artichokes from the ground; Krainova, 1951). Damage was generally insignificant. When populations were high, wisent may have suppressed undergrowth (Zablotskii, 1957).

The conservation of wisent commenced in the 1540's. There is no doubt that this measure promoted the conservation of Belovezh 417 wisent right up to the twentieth century. In the 1860's, as soon as the existence of Caucasian wisent was confirmed, their killing was prohibited. However, the ban was not implemented for quite some time and was later enforced to some extent only in the territory of Kuban Game Farm, where poaching of wisent attracted a fine of 500 rubles. The creation of the Kuban Game Farm and Belovezh Forest were extremely unpopular among the local populace; then failed to save and merely postponed the extinction of wisent under natural conditions.

At present throughout the world only a small number of pure-blooded wisent have survived (these usually now include hybrids with wisent blood of not less than 15/16 since these animals are practically indistinguishable from true wisent in external appearance). In the Soviet Union substantial work has been done, mainly in preserves, on the restoration of wisent by selective crossbreeding. An international society for the preservation of wisent was set up as early as 1923.

The economic importance of wisent has yet to be realized. What is more important now is to save the species from total extinction and to restore its population to a level beyond endangerment. (A.N.)

Subfamily of Gazelles

Subfamily Antilopinae Baird, 1857

Animals of medium, small, and very small size, extremely slender and light build, with a straight back, thin, slender and usually long legs, proportionately thin, sometimes elongated neck, and a small, slender head set high.

Lateral hooves (of digits II and V) vary in development and sometimes absent. In some (mountain) forms even hooves of medial digits highly reduced.

Facial part of skull, with some exceptions, developed relatively poorly (short), forehead small, and occipital part highly developed. Skull pneumatization slight or absent. Preorbital depression on lacrimal usually moderate in size, sometimes very large (in some cases encompasses even part of maxillae), or altogether absent. Ethmoid pit usually small, sometimes altogether absent, or prominent. Premaxillae adjoin nasals or do not reach them; sometimes (as a result of proboscis-like nasal elongation) nasals highly shortened and premaxillae elongated.

Cheek teeth brachyodont, with sharply ridged prisms, sometimes fairly hyposodont, but also with sharply ridged prisms, and compressed prisms. Anterior pair of incisors enlarged in the form of an asymmetrical spatula. Dental formula usually:

$$i\,\frac{0}{3},\quad c\,\frac{0}{1},\quad pm\,\frac{3}{3},\quad m\,\frac{3}{3} = 32.$$

(sometimes anterior pm very small) but as an exception pm $\frac{3}{2} = 30$ or pm $\frac{2}{2} = 28$ is possible. Sometimes upper canine prominent.

Horns diverse in type but invariably set on anterior surface of frontals with bases close together. Transverse section of horn circular, more rarely with a small anterior rib. Horns for the most part thin and moderate in length or quite long with transverse annular ridges or transverse prominences on anterior portion of basal half; horns lyrate to some extent with basal part of each projecting somewhat forward. Sometimes horns bent back initially and then forward, or turned upward and then sideways, or twisted in a straight heteronymous spiral. In some species horns in form of short, 418 smooth, and sharp stubs set straight or slightly bent back. Keratin black. Both sexes usually bear horns, which are slightly smaller, weaker, and simpler in females than males, or females may be hornless.[66]

Tip of muzzle not enlarged, wholly (up to posterior margin of nostrils) bare, or sometimes partly or densely covered with hair; sometimes muzzle extends in the form of a proboscis but is not swollen. Skin glands highly developed, and facial (preorbital), inguinal, and glands on limbs (carpal, knee cap, tarsal, and hoof) occur in most species. Exceptionally glandular collections present on back, behind horns, or on rear surface of shank. Hoof glands developed to various degrees and invariably present on fore and hind limbs. In different species or groups of species certain glands may be absent, or occur in various combinations, or may be developed to very different degrees (especially preorbital glands).[67] Tail short (sometimes even in the form of a short stump), or moderate in length; exceptionally, fairly long, almost reaching calcaneal joint, but without tassel at the end and uniformly covered with hair, and sometimes bare at the tip. Dewlap absent.

---

[66] In such species some percentage of females may grow hornlets of irregular form during old age.

Pelage short, dense and uniform in length throughout body. Color usually uniform light yellow ("desert-like"), or shades of brown with a much lighter base. Transverse bands on trunk absent. Sometimes facial pattern of longitudinal light and dark color bands, characteristic of gazelles, present. Sexual dimorphism of color absent with some exceptions (*Antilope*); females usually smaller than males, with much weaker horns or without them; in some species, however, females larger than males. Teats two or four.

The subfamily includes a distinct group called gazelles, which are extremely similar in general appearance and size (*Gazella, Procapra, Antidorcas*), i.e., the most typical antelopes, with some proximate forms, and all pygmy antelopes, which also form a fairly monotypic group. Pygmy antelopes constitute a typical group and differ from gazelles in general appearance, but there can be no doubt about their taxonomic proximity. On the whole, subfamily Antilopinae, compared with other subfamilies of Bovidae (specially Bovinae), can be considered relatively monotypic.

Members of the subfamily are inhabitants of deserts, steppes, forest-steppes, and exceptionally, of forests. Some are montane species and even highly specialized inhabitants of rocky areas. Some small species live in grass, similar to hares. Most are extremely mobile, fleet-footed, and jumping animals, capable of very high speeds. They live in groups and herds which are sometimes large, even huge.

The range of the subfamily is extensive and forms a single block in the Old World. Antilopinae occur in the whole of Africa up to the Cape (excluding Madagascar), Arabian Peninsula including the Syrian region of United Arab Republic and Palestine, Iraq, Iran, Afghanistan, Baluchistan, India (from the foothills of the Himalayas to Cape Comorin [Kanya Kumari] in the south, and up to Bengal and Assam in the east (but absent in Ceylon [Sri Lanka]), Middle Asia, in the north roughly up to the line of the northern Ustyurt in the Tarbagatai (see section on goitered gazelle), Dzhungaria, Kashgaria, Mongolia, Trans-Baikal (see section on Mongolian gazelle), western part of

---

[67] Combinations, degree, and form of glandular development (glandular field or sac) are vital in taxonomic diagnosis.

China including the western half of northeastern China, Chihli, Kansu, Szechwan, and Tibet. They are absent in the Himalayas and some other montane regions. In a purely geographic context Antilopinae represent an African-South Asiatic group.

Among the subfamilies of Bovidae Antilopinae evidently stand closest on one side to the subfamily of goats (Caprinae) and on the other to antelopes of the subfamily Hippotraginae (Africa; 13 genera), among them the tribe Reduncini ("water goats"; 4 genera, 11 species). Some taxonomists even include the latter among the Antilopinae.
419 The links in all directions are through gazelles (Antilopini). Pygmy antelopes (Neotragini) are more independent. In general, however, the systematic relations of the subfamily, as also of some other "antelopes", are now fairly well understood.

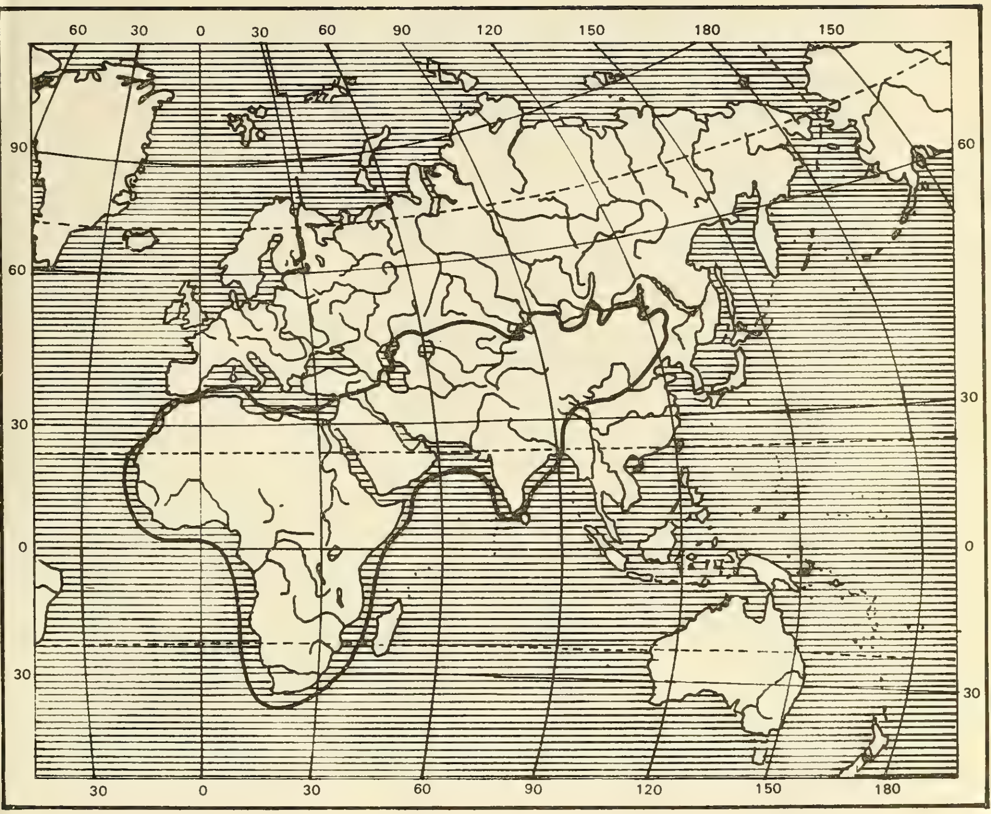
Species of Antilopinae are known from Asia from the Lower Pliocene onward.[68] These also include forms of the extant genus *Gazella* or those close to it. They developed evidently in the Near East. Throughout the Pliocene Antilopinae are known only in Europe and Asia, where they flourished and occupied a prominent position among other cavicorns. In Africa, at the place of their present greatest diversity and abundance, Antilopinae are known only from the Pleistocene and appeared there not before the end of the Pliocene. In Europe there were no Antilopinae whatsoever during the Pleistocene. Thus, based on their history, Antilopinae should be considered Eurasian in origin, and a comparatively recent mammalian group in Africa. The origin of the group should evidently be placed at the end of the Miocene since members definitely existed in the Lower Pliocene. The immediate ancestors of Antilopinae have not yet been traced.

The subfamily includes some fossil genera but all belong to Recent groups (tribes, see below). Antilopini (eight genera—Europe, Asia, and Africa) are more abundantly represented in the fossil state. Only one Pleistocene African genus is known, from Neotragini, but several forms of Recent genera are common. Thus the above discussion of the history of the group concerns mainly Antilopini. Neotragini, it would appear, should be regarded as a relatively new, purely African branch of the subfamily.

420 Antilopinae are presented here in a very broad sense, i.e., include Aepycerotinae, Oreotraginae, Neotraginae, Madoquinae, Antilopinae (= Gazellinae) of various researchers, and genus *Ammodorcas*. In spite of the diversity of the species constituting the subfamily, the latter represents a fairly natural group. The division of this group

---

[68] According to other data, from the Upper Miocene.



419 Fig. 131. Range of the subfamily of gazelles, Antilopinae, V.G. Heptner.

into further subfamilies, often monotypical, undertaken by several taxonomists quite recently, is largely formal and based partly on an exaggerated evaluation of certain special features (presence or absence of certain glands, etc.).

Fairly significant differences are known between the two main groups—gazelles and pygmy antelopes. This, however, is a divergence only within the subfamily and two corresponding tribes may be assumed: Neotragini—including the groups Oreotraginae and Madoquinae of various taxonomists; and Antilopini—comprising Antilopinae, Aepycerotinae, and *Ammodorcas*. The first group includes true gazelles (genera *Gazella, Procapra,* and *Antidorcas*), the closely related dibatag (*Ammodorcas*), impala (*Aepyceros*), gerenuk (*Litocranius*), and blackbuck or screw-horned antelope (*Antilope*). The latter group includes the pygmy antelope, dik-dik, oribi, klipspringer, beira, suni, royal antelope, and others, i.e., genera *Oreotra-*

gus, Ourebia, Raphicerus, Neotragus, Nesotragus, Madoqua, Rhynchotragus, and *Dorcatragus.* Evidently Antilopinae should be regarded as more specialized, although several relatively primitive features of Neotragini are probably associated with the "infantile" features of these extremely small animals.

The systematics of the subfamily (especially of Antilopini) in relation to its specific composition has been clearly elucidated in recent years and the classification of the group may be considered fairly simple. Yet a tendency to further subdivide genera (especially those of Neotragini) still persists.

There are 24 genera in the subfamily; of these, 9 are extinct and 15 extant (about 28% of present-day genera of the family). The total number of species is 34: among Neotragini—*Madoqua* (4 species), *Ourebia* and *Raphicerus* (including *Nototragus*) (1 and 3 species), *Neotragus* (including *Hylarnus*) and *Nesotragus* (2 species each), *Oreotragus* and *Dorcatragus* (1 species each), and *Rhynchotragus* (2 species). Species among Antilopini are: *Gazella* (12), *Procapra* (2), and *Antilope, Litocranius, Aepyceros, Ammodorcas,* and *Antidorcas* (1 each). These represent 32.3% of present-day species of Bovidae.

Of the 15 present-day genera, 12 are purely African, 2 purely Asian (*Antilope* and *Procapra*) and one Afro-Asian (*Gazella*). Of the 34 present-day species (15 Neotragini and 19 Antilopini), 5 are purely Asian (2 *Procapra,* 1 *Gazella,* and 1 *Antilope*), 3 Afro-Asian (*Gazella*), and the rest purely African. Thus present-day Antilopinae represent a distinct African group and the dispersal of all Neotragini is confined to Africa.

Species of this subfamily are table and game animals. Some are known hosts of dangerous parasites of man and domestic animals (Africa).

The Russian fauna includes two genera (13.3% of present-day genera of the subfamily) and two species (6.0% of species of the subfamily), constituting 0.6% of all species of Russian fauna.

In the Soviet Union these animals inhabit deserts, semideserts, and often the steppes. They form herds, sometimes large ones, and dwell in open expanses, sometimes in foothills.

Russian genera represent game and table animals. At places, hunting them is prohibited. (V.H.)

Genus of Gazelles

Genus *Gazella* Blainville, 1816

421 1816. *Gazella.* Blainville. *Bull. Soc. Philom. Paris,* p. 75. *Capra dorcas*

Linn.[69]

1951. *Trachelocele.* Ellerman and Morrison-Scott. *Check-list of Palearct. and Indian Mammals,* p. 390. *Gazella subgutturosa* Pallas. Described as a subgenus. (V.H.)

Species of large and moderate size. Neck not elongated.

Lateral hooves (of digits II and V) present and hooves of medial digits developed normally.

Facial part of skull not elongated or enlarged and profile of frontonasal region relatively straight. Preorbital depression of lacrimal well developed. Ethmoid pit present; nasals and premaxillae of normal length; latter usually do not reach former. Nasals have a notch on the anterior edge. Tympanic bulla large.

Cheek teeth brachyodont. Dental formula:

$$i\frac{0}{3},\ c\frac{0}{1},\ pm\frac{3}{3},\ \ m\frac{3}{3} = 32.$$

Horns long and with distinctly visible transverse annular prominence almost throughout their length (terminal portion smooth). Horns lyrate to various degrees. Basal part of each horn usually slightly turned forward, midpart backward and outward, and end part turned in or in and forward. In a few cases horns turn upward initially and later backward and outward. Horns, except for one species (*G. subgutturosa*), also characteristic of females.

Tip of muzzle not elongated; covered with hair, except for small irregular patch in space between nostrils. Well developed, saccate preorbital, femoral, and carpal glands ("knee cap"). Hoof glands on fore and hind legs well developed and deeply set. Tail relatively long.

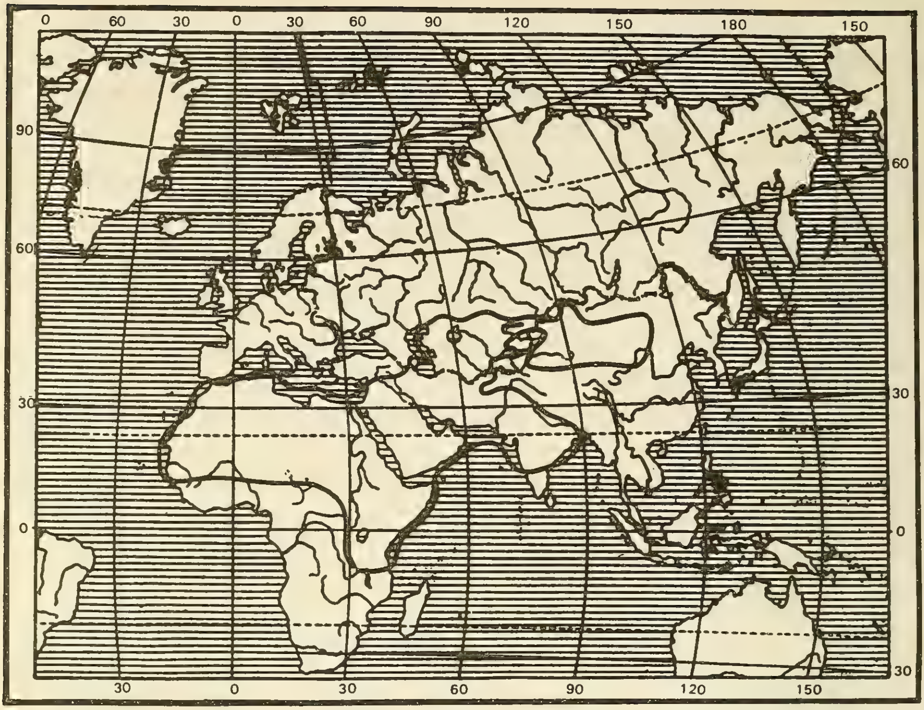
Color sandy or brown, with white speculum on rear surface of thigh; latter generally small and does not rise above base of tail or does 422 so only insignificantly. On the sides sometimes a very dark longitudinal field occurs along the color boundary between the upper and lower body; sometimes this field is very light in color. Characteristic facial pattern of gazelles in the form of light-colored bands running from the base of the ear to the nose, sometimes darker in color, variously developed, sometimes even absent. Sexual color dimorphism absent. Teats two.

The genus includes animals which are most typical of gazelles in general appearance.

Gazelles are inhabitants of deserts, steppes, and forest-steppes.

---

[69] According to a decision of the International Nomenclature Committee (resolution 108) the name *Gazella* should be used with reference not to Lichtenstein (1814) or Pallas (1769), as done by some taxonomists, but in the manner adopted here.



421 Fig. 132. Geographic range of gazelle, *Gazella* Blainv. V.G. Heptner.

They live in herds and form large groups in certain seasons.

The range of the genus covers North Africa and the northern part of East Africa, in the south to Senegal-Gambia, northern Nigeria and northern Cameroon, the region of Ubangi-Chari, southern Sudan, Uganda, Kenya, and Tanganyika. In Asia members of the genus cover all of the Arabian Peninsula, including the Syrian region of the United Arab Republic and Palestine, Mesopotamia, Iran, eastern Trans-Caucasus, Afghanistan, Middle Asia roughly up to the line of the northern Ustyurt-Tarbagatai (see section on goitered gazelle), Kashgaria, Dzhungaria, Mongolian Republic, part of Inner Monogolia, northern Tibet (Tsaidam), northwestern, northern and central India (Baluchistan, Sind, Punjab, Rajasthan, Cutch, Kathiawar, United Provinces [Uttar Pradesh] and Central Provinces [Madhya Pradesh]) and southern India roughly to 15°, i.e., slightly south of the Kistna [Krishna] River.[70]

Gazella represent a well-isolated group, occupying a central position among Antilopini; taxonomically they are the most typical gazelles. The genus *Procapra* (Mongolian gazelle) stands closest to the genus *Gazella.* Some taxonomists consider the former only a subgenus of *Gazella;* this view is well founded. To some extent the Asiatic *G. subgutturosa* (goitered gazelle) could be considered a connecting link between the two groups. In any case the differences between *Gazella* and *Procapra* are less than between *Gazella* and other genera of Antilopini (*Ammodorcas, Antidorcas, Litocranius,* and *Aepyceros*—all monotypic), which contain sharply differing forms.

---

[70] References to Nepal are evidently erroneous.

The genus *Gazella* is included in "old" genera and its members known even from the Lower Pliocene (according to some data from the Upper Miocene—*G. deperdita*) and several species from the Pliocene, being more widely dispersed then than now (England). The direct ancestor of the genus has not been established.

In recent years the composition and interrelations of the species within the genus have been fairly well understood. The number of species has been drastically reduced (formerly 23 to 30). Recently the genus was divided into three subgenera: *Gazella* (type *G. dorcas*), *Nanger* (type *G. dama*), and *Trachelocele* (type *G. subgutturosa*).

Subgenus *Trachelocele* is characterized by absence of horns among females and the swelling of the larynx in males in the period of rut to form a characteristic protruding "goiter". Other characteristics are the same as in *Gazella* s. str. The separation of these subgenera is not well founded and, as pointed out earlier, subgeneric relations are better defined between *Gazella* (i.e., the three subgenera listed above) and *Procapra.*

There are 12 or 13 species in the genus, constituting 35 to 38% of the species of the subfamily—1 species in subgenus *Trachelocele,* 3 in subgenus *Nanger,* and 9 in *Gazella.* One species is purely Asiatic (*G. subgutturosa*), three Afro-Asian (*G. dorcas, G. leptoceras,* and *G. gazella;* their ranges run into the Arabian Peninsula, Iran, and India), and the rest African (*G. rufifrons, G. tilonura, G. pelzelni, G. spekei, G. t*[*h*]*omsoni, G. dama, G. soemmeringei,* and *G. granti*). Thus, although Asian in origin, the genus should now be considered predominantly African from a geographic point of view. Zoogeographically this group falls in the desert belt of the southern Palearctic.

Gazelles are game animals.

In the Soviet Union one subgenus, *Trachelocele,* and one species, *G. subgutturosa* Gueldenstaedt, 1780 (goitered gazelle), are found, representing 8.0% of species of the genus and about 0.3% of species of Russian fauna.

423 This form is a desert and semidesert animal in Middle Asia and

the Trans-Caucasus. It is a game animal but hunting is prohibited at some places. (V.H.)

11. DZHEIRAN[71]

Gazella subgutturosa Gueldenstaedt, 1780

1780. *Antilope subgutturosa.* Güldenstaedt. *Acta Acad. Scient. Petropolitanae,* 1778, tab. 1. p. 251. Steppes of eastern Trans-Caucasus.[72]

1843. *Antilope dorcas* var. *persica.* Gray. *List. Mamm. Brit. Mus.,* p. 160. Iran. 1900. *Gazella subgutturosa typica.* Lydekker. *Great and Small Game of India,* p. 180. Iran.

1900. *Gazella subgutturosa sairensis.* Lydekker. *Great and Small Game of India,* p. 184. Saur range in Dzhungaria.[73]

1910. *Gazella subgutturosa seistanica.* Lydekker. *Nature,* vol. 83, p. 202. Seistan, eastern Iran.

1956. *Gazella subgutturosa gracilicornis.* Stroganov. *Zap.-Sib. Filial (Ak. Nauk SSSR). Trudy Biol. Instituta,* no. 1, p. 17. Vakhsh valley. Tadzhikistan. (V.H.)

424

Diagnosis

G. subgutturosa is the only species of genus *Gazella* found in the Soviet Union.

Description

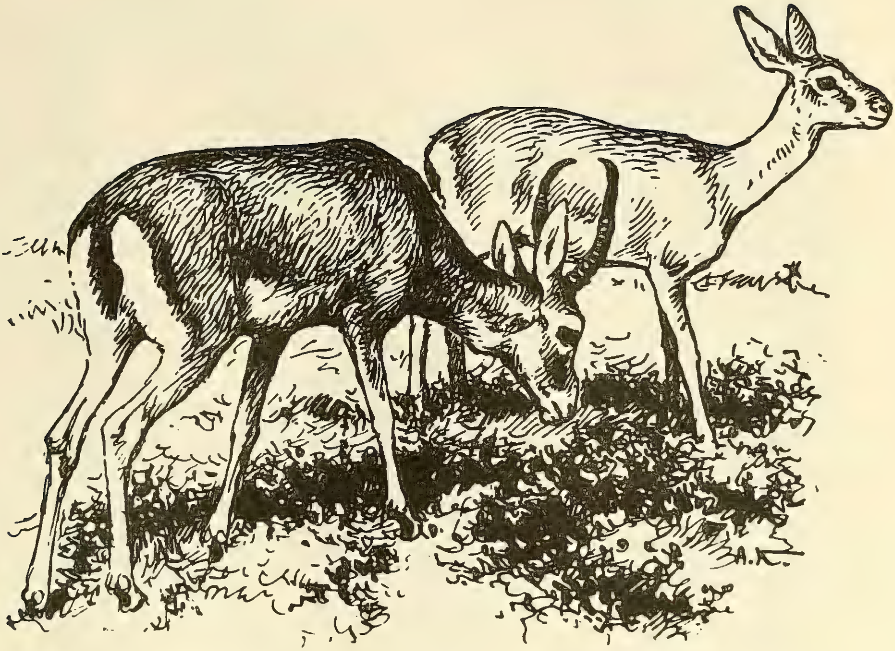
Antelopes of moderate size and light build, standing on long, slender legs. Withers slightly lower than, or at the same level, as sacrum. Body length equal to, or slightly less than, height at withers. Head small and neck relatively long. During rut larynx of

---

[71] An Iranian name. In Central Asia it is known as "Karakuiryuk" (Kazakhstan and Kirghizia) and "akhcha-keik" (Turkmenia) [English, goitered gazelle].

[72] References to Persia or occasionally "Persia, probably Bussora" (Flerov, 1935) as the type locality, based on Lydekker's assumption (1914), are evidently erroneous (Stroganov, 1956). Güldenstaedt's material came from the Trans-Caucasus, possibly even from the environs of Tbilisi. "Bussora" should evidently be regarded as "Basra" or, as sometimes written in Russian, "Bassor" (archaic form; English "Bussora"). Güldenstaedt did not visit Mesopotamia and could not have had material from there. What is more important, in the first half of the eighteenth century a significant part of eastern Trans-Caucasus fell within the territory of Iran.

[73] Not Lake Sairam-Nor, as pointed out by Stroganov (1956).



423 Fig. 133. Goitered gazelle, *Gazella subgutturosa* Güld. Sketch by A.N. Komarov.

males protrudes from throat in form of a small goiter. Small patch at end of muzzle, between nostrils, covered with hair. Eyes large, black, and bulging. Tail relatively long (longer than ears) and distinctly bicolored; sandy-brown from basal part upward and black or dark brown at tip, sometimes with a tassel of whitish hair. Hair covering tail bristly and longer than that on trunk. Preorbital, femoral, carpal, and hoof glands well developed.

Horns black and lyrate. Set close at base, they later diverge sideways and turn backwards, while their ends turn in and slightly forward. For the most part, apart from tips, horns with wavy annular prominences; latter may number 26 to 28 (more often 16 to 20) in adults. Females usually without horns; small stumps up to 50 mm long have been recorded in rare cases.

Hooves black, narrow, and pointed in front. Length of front hooves 50 to 56 mm; width almost one-half length. Front hooves slightly (by 1.2 to 3.0%) larger than rear ones.

There is no distinct separation of the hair into guard hair and underfur. Winter fur 3.0 to 5.0 cm, and summer fur up to 1.0 to 1.5 cm long. Hair on muzzle and legs shorter than that of trunk. In females small tassels of longer hair occur around the horns.

In summer coat color of upper body and sides sandy-brown. Under-body, neck, and inner surface of legs white. Anterior and exterior part of legs, except for lowermost parts, same color as trunk; sections above hooves darker or brownish. White speculum does not rise on the back above base of tail. Along color boundary of upper and lower body portions, a dark field occurs on the sides in the form of a longitudinal band. Color scheme on face distinct only in young; dark brown patch on nose bridge and two dark bands extending in front on eyes; from light-colored circum-ocular ring above the eye rise light-colored bands; similar bands run along cheeks and lips, converging toward upper bands on nose. With age, only the short dark bands in front of eyes remain from this pattern; top of head becomes lighter in color. Winter coat on back and sides lighter-colored than summer sandy-gray coat of different shades. Design on face faint and dark bands on muzzle grayish-smoky.

Very large tympanic bullae and deep notches in the anterior portion of nasals, throughout their width, are characteristic features; preorbital pits (fossa lacrimalis) are also distinct. (For more details of skull, see description of genus).

Measurements: body length of males 110 to 116 cm and females 93 to 110 cm; height of males at withers 64 to 75 cm and females 60 to 68 cm; tail 16 to 20 cm; ear 8 to 13 cm; length of horns measures along curvature 25 to 41 cm; weight of males 23 to 33 kg and females 18 to 20 kg. Maximum skull length of males 172 to 224 mm and of females 182 to 208 mm. (A.B.)

Taxonomy

This species occupies a central position in the genus. Goitered gazelles have several primitive features of build, particularly the absence of horns in females. Yet, being an inhabitant of the desert (hard substratum), goitered gazelle are a highly specialized form. Specialization is reflected in the very high load bearing of the hooves, low angle of the front surface of the hoof, and maximum elongation and thinning of metatarsals and metacarpals (Vereshchagin, 1939). (A.B.)

425 Geographic Distribution

Goitered gazelles inhabit the deserts of the eastern Trans-Caucasus, the Near East from the valley of the Euphrates to Baluchistan, Afghanistan, Middle Asia, southern Kazakhstan, Dzhungaria, Kashgaria, Tsaidam, and northern Tibet, the Gobi in the north to Southern Mongolia, Ala Shan, and Ordos.

Geographic Range in the Soviet Union

The range in the Soviet Union (reconstructed) is divided into two parts—an extensive Middle Asian and a small Trans-Caucasus. That part of the range of the goitered gazelle in the Kur'-Araks lowland of eastern Trans-Caucasus is totally isolated from the rest of the distribution area of the species, this isolation having evidently occurred in the prehistoric period. The prevalence of extremely ancient irrigated agriculture in the plains of eastern Trans-Caucasus (from the fourth to the fifth centuries A.D.) and the absence of older sources of information about the distribution of goitered gazelle, hinder reconstruction of the range there before the advent of man. However, the areas occupied by goitered gazelle at the end of the nineteenth century evidently were close to corresponding areas of early epochs. Sharp range contraction occurred only in the twentieth century (Vereshchagin, 1939). Range contraction has been particularly intense in the last 25 to 30 years; the range had already become patchy in the 1930's.

The northwestern limit of the occurrence of goitered gazelle at the end of the nineteenth century lay in the valley of the Kur' River at Avchal (10 km west of Tbilisi) up to which typical swallowwort desert extended (Radde, 1899). In the southwest goitered gazelle were probably present in the Araks valley between Nakhichevan' and Erevan (Satunin, 1905) but vanished from that section in the last century itself. The northeastern corner of the range lay slightly north of Apsheron, where judging from the nature of the topography, goitered gazelle probably reached 41° N lat. Even quite recently, in the 1930's, these gazelle were seen around Nasosnaya and Kiyaza railway stations, inhabiting also the central sections of the Apsheron Peninsula (Vereshchagin, 1939). In the southeast goitered gazelle lived in the Mugan Steppe, that falls within the Soviet Union as well as Iran. The Kur'-Araks lowland could be regarded as the lone northwesternmost isolated section of the range, the closest to it being the Iranian plateau to the south. Only later, in the Recent period, did it split into a series of small sections or spots, which by the mid-1930's numbered ten (Vereshchagin, 1938, 1939, and 1947).

The extreme northwestern section falls in the interfluve of the Iora and Kur', whence goitered gazelle penetrated earlier as far as to

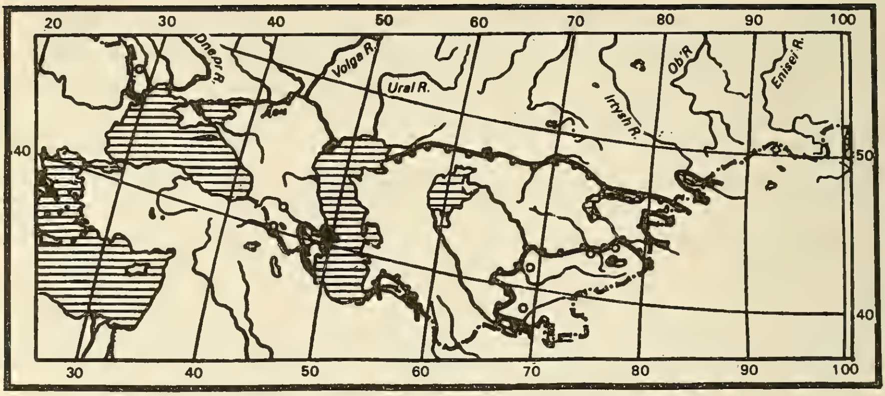


Fig. 134. Geographic range of goitered gazelle, *Gazella subgutturosa* Güld. in the Soviet Union. A.G. Bannikov.

Tbilisi. Even in the mid-1930's the western boundary of this section ran along the meridian of Kazakh station. Later gazelle were sighted even in the eastern part of this region, around Lake Kadzhiris-Tba and in the valleys of the Erik-Tar and Dzheiran-Chela (Vereshchagin, 1939 and 1947). More northeast, in the interfluve of the Iora and Alazan (Shirak steppe), goitered gazelle were common early in 426 the century. At present, perhaps, they are preserved at the center of the steppe and in its southeastern corner. Slightly more south, in the Adzhinour steppe to the east of the confluence of the Alazan and Kur', these gazelle probably survived close to Lake Adzhinour. From 1932 to 1935 an intense destruction of gazelle and cultivation of the steppe took place, but in the 1940's they were still seen in the fields among cereal crops (Vereshchagin, 1947). Even more south, in the valley of the Kyurak-Chai to the east of Kirovobad where gazelle were once common (Kessler, 1878), they are now absent. Possibly they still survive northeast of Evlakh, on the southern slopes of the Bozdag range.

The Mil'sk-Karabakh steppe until quite recently was one of the largest habitats of goitered gazelle in Trans-Caucasus. There were about 1,500 animals in an area of around 2,000 km^2 in 1936 (Vereshchagin, 1939). Later, cultivation in Mil'sk steppe intensified and the area inhabited by gazelle decreased sharply. In the Mugan steppe gazelle were formerly widely distributed (Satunin, 1921 and 1923). In the mid-1930's they were confined mainly between the Azizbek and Lenin canals and also along the Iranian boundary from Belyasuvar to Araks (Vereshchagin, 1939); a few were sighted in the Sal'yan steppe. In the Shirvan steppe, much of which is currently cultivated

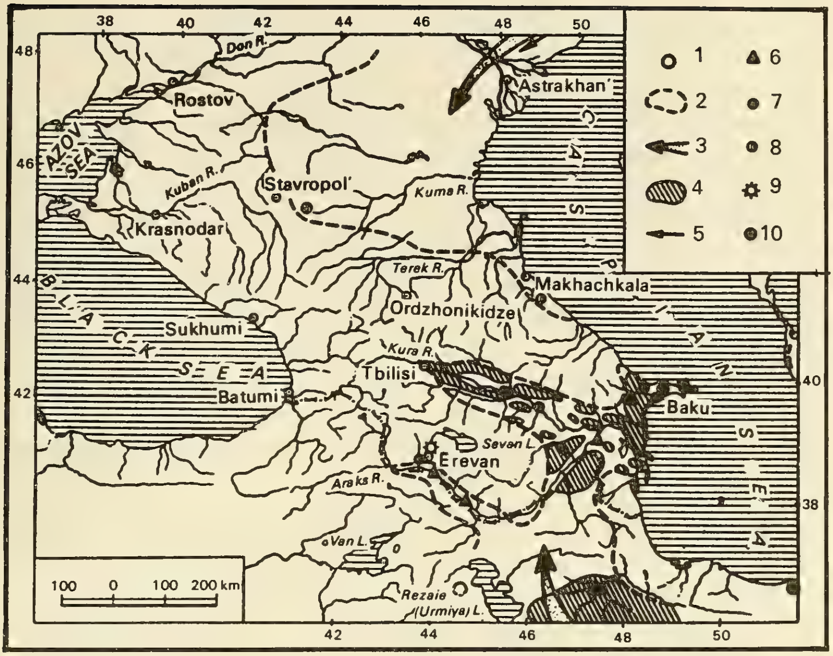

38
40
42
44
46
48
50
48
46
44
42
40
38
Don R.
Rostov
AZOV SEA
Kuban R.
Stavropol'
Krasnodar
Kuma R.
Astrakhan'
CASPIAN SEA
Terek R.
Makhachkala
Ordzhonikidze
BLACK SEA
Sukhumi
Kura R.
Tbilisi
Batumi
Baku
Sevan L.
Erevan
Araks R.
Van L.
Rezaie (Urmiya) L.
100 0 100 200 km
1
2
3
4
5
6
7
8
9
10

Fig. 135. Range of goitered gazelle, *Gazella subgutturosa* Güld. in the Caucasus. From Vereshchagin, 1959.

1—Pleistocene; 2—maximum possible range in Holocene; 3—probable course of settlement; 4—range in early twentieth century; 5—occasional excursions; 6—information available in literature for seventeenth to nineteenth centuries; 7—thirteenth to ninth centuries B.C.; 8—tenth to seventh centuries B.C.; 9—3000 B.C.; 10—Holocene.

and irrigated, goitered gazelle inhabit only the eastern and southeastern parts, close to Lake Karasu and Adzhikabul, and also in the Pirsagat River lowlands and adjacent regions.

Finally, the northeasternmost section adjoining the Apsheron Peninsula (Kabristan) represents one of the most extensive regions in which goitered gazelle live east of the Trans-Caucasus. In any case this was true in the 1930's and 1940's when about 1,200 animals lived
427 there in an area of about 2,000 km^2. From there gazelle penetrated into the Apsheron Peninsula and even farther north (Vereshchagin, 1939 and 1947).

East of the Caspian the northern boundary of distribution of goitered gazelle traversed Kazakhstan. The northwestern limit of the permanent habitation of these animals in Kazakhstan was the Emba River; in summer gazelle even now are usually sighted in the lower reaches of the Emba. Instances of winter finds are known in the Volga-Ural interfluve region.

Goitered gazelle are regularly seen north of the Ustyurt Chink, in the region of Irgiz and Chelkar-Tangiz, reaching to 48° N lat. Extending eastward along the 48th parallel, the range boundary bypasses the Ulutau mountains to the south and runs along the upper course of the Sary Su River and the northern outskirts of the Bet-Pak-Dala. In the triangular section between the railway stations Dzhezkazgan-Zharyk and Zharyk-Mointa-Balkhash goitered gazelle are common in summer; sometimes they cross to the north of the Dzhezkazgan-Zharyk railway line. East of the town of Balkhash, on the northern bank of the lake, gazelle are rare now but were regularly sighted in the past. From the eastern end of [Lake] Balkhash the range boundary used to run along the northern outskirts of the Alakul' depression and from there, through the Dzhungarian Gateway*, left the Soviet Union to enter China (Antipin, 1941; E. Strautman, 1953; A.A. Sludskii). Comparatively recently, goitered gazelle disappeared from the Lake Zaisan depression (Sedel'-nikov, 1903; Khakhlov, 1928; Finsh and Brem, 1876), which they had penetrated along the Chernyi Irtysh valley from Dzhungaria (China).

In the southern part of the Soviet Union goitered gazelle inhabit all of Turkmenia except the montane parts of the Kopet-Dag, Balkhan, Gyaz'-Gyadyk, and Chengurets mountains (between Kushka and Murgab) (V.G. Heptner). Farther east they penetrate along the Amu-Darya up to the lower reaches of the Pyandzha and Vakhsh Rivers in Tadzhikistan (Flerov, 1935). However, along the foothills the boundary circumscribes all of the montane region of Middle Asia. From the Amu-Darya, along the foothills of the Zeravshan range and the Nuratau, it turns toward the Syr-Darya, later bypasses Karatau, and again turns eastward along Chuisk-Muyunkum (Kashkarov, 1925).

Along the Chuisk valley goitered gazelle formerly penetrated far southeast, as far as the Semizbel' Plateau, but they vanished from the western parts of Chuisk valley within Kirghizia long ago, probably even in the last century, since the last two generations of people there could not recollect goitered gazelle (D. Dement'ev, 1935). In the Lake Issyk-Kul depression this gazelle was quite common along the northern bank of the lake. In the mid-1930's it was on the verge of extinction there. It may even have become extinct but reentered the depression from the Syugotin valley to the north. At present (1958) gazelle occur from the Torus and Ulakhal Rivers to the Ortokoisa River, i.e., they extend for 50 to 60 km along the shore of the lake

---

*A pass between the Dzhungarsk Alatau and Barlyk mountains on the border with China—Sci. Ed.

(P.P. Tarasov). Goitered gazelle inhabit the Chu-Ili mountains and southeast of them, the Syugotin and Dzhelanash valleys. Farther east the range boundary runs along the broad valley of the Ili directly into China. Goitered gazelle are found regularly, but in small numbers, in the foothills of the Trans-Ili Alatau and the Ketmen' range.

Goitered gazelle are found mostly in summer north of the Chu River and the lower reaches of the Syr-Darya, while in the Ili and Sary Su river valleys they are seen year-round. In the Ferghana valley they inhabit (inhabited) the foothills of the Kuramin range eastward to Tyurya-Kurgan; probably they were formerly present in central Ferghana also (Malenkov, 1958).[74]

At several places within the range boundaries outlined above, goitered gazelle have disappeared or are disappearing, but adequate data are not available for reconstructing a detailed picture of their distribution.

Geographic Range outside the Soviet Union

In the northwest goitered gazelle inhabit the Iranian plateau (the Trans-Caucasian population is isolated). In the southwest they reached (? reach) the Euphrates. They are encountered in the Iran-Afghanistan deserts: Dasht-i-Kevir, Dasht-i-Lut (Iran), Dasht-i-Markakh, and Registan (Afghanistan). In the southeast they
428 evidently reach northern Baluchistan within Pakistan. In Central Asia, east of 75° E long., the southern boundary of the range traverses the foothills of the Kun'lun. Goitered gazelle are present in Tsaidam between the Nan Shan and Kun'lun, and penetrate the high Lake Kukunor basin but are absent in the eastern Nan Shan. The southern boundary of the range of these animals twice intersects the northern curvature of the Hwang Ho and, extending at places to 115° E long., becomes the eastern boundary. The easternmost point of the distribution of goitered gazelle falls roughly at the intersection of 115° E long. and 43° N lat. From there, turning west, the range boundary becomes the northern boundary and, gradually rising, runs into the Mongolian Peoples' Republic (Welles, 1913; Raymond, 1932; Allen, 1940). In Mongolia the boundary of distribution of goitered gazelle runs east to west as follows: from the point of intersection of the state boundary, roughly at 112° E long., it ascends north toward Baishinta. Along deserted dry valleys the animals

---

[74] Horns and bones of goitered gazelle were found at the Chustkaya site (bronze age) in 1955 (Malenkov, 1958).

penetrate there up to 46° N lat. Later, following roughly 46°, the range boundary runs toward Choire and descends toward Mandal-Gobi and Delger-Khanghai range. Intersecting the Ongin-Gol River, the boundary again extends along the basin of the Gobi lakes to the southern bend of the Dzabkhyn River. Still more northward goitered gazelle are seen in the Shargiin-Gobi and the basins of the large western lakes to the Lake Khirgiz-nur depression, i.e., to 49° N lat., which represents the northernmost point of the range of the species. Encircling Mongolian Altai along the slopes of the main mountain range, the boundary leaves the country westward (Bannikov, 1951 and 1954). Farther away, even within China, the northern boundary of goitered gazelle extends along the foothills of the Mongolian Altai right up to the Lake Zaisan depression. Quite naturally, within the range outlined above, goitered gazelle were absent along the major elevations of the Gobi Altai and other mountain systems.

Quaternary finds of goitered gazelle lie within the limits of the present-day range. In the Paleolithic fauna of Troitskosav (western Trans-Baikal) there were no goitered gazelle, but another species of the same genus (Gromov, 1948). (A.B.)

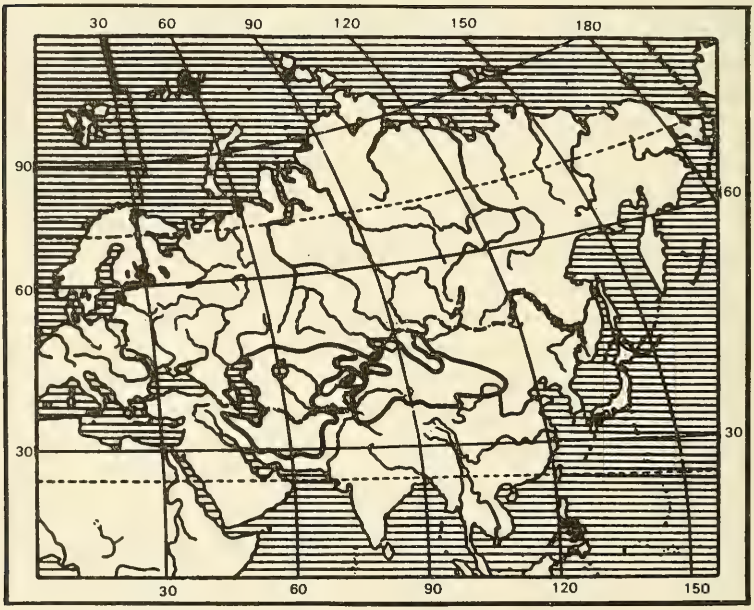


Fig. 136. Reconstructed range of goitered gazelle, *Gazella subgutturosa* Güld. A.G. Bannikov.

Geographic Variation

Geographic variation in goitered gazelle has not been studied adequately; nevertheless there is very little variability compared to other 429 Asian desert-steppe ungulates. The reasons for this are poorly developed barriers in the range of the species and extensive migrations of the animals. Of the eight forms described, only one (*reginae* from Tsaidam) is based on a fairly thorough revision of species variability as a whole (Allerberg, 1931). This revision demonstrated the untenability or extreme subtlety of all the remaining forms known at that time. Even the Tsaidam form living in an extremely unusual environment and in geographic isolation from the rest, is only weakly differentiated.

It is quite possible that the Trans-Caucasian goitered gazelle, evidently isolated from other members of the species, represents a separate but not sharply differentiated form. Throughout the rest of the range in the Soviet Union there is obviously only one form.

Goitered gazelle, *G. s. subgutturosa* Gueldenstaedt, 1780 (syn. *typica, gracilicornis*). Description given above pertains to this form.

Found almost throughout the range of the species in the Soviet Union.

Outside the Soviet Union found in the Near East and Central Asia, except Tsaidam.

If the taxonomic independence of the Trans-Caucasian population is established (color of the animals from there somewhat darker), then this form only should be acknowledged as the nominal form. Naming the Russian-Middle Asian-Kazakhstan goitered gazelle requires special systematic and nomenclatural studies. If this population is homogeneous, which is highly probable, the names given above as synonyms (apart from *typica* and *gracilicornis*) could be used. These names must be taken into consideration at any rate if the animals of east and west should prove different varieties.

Outside the Soviet Union, *G. s. reginae* Adlerb., 1931 (Tsaidam, northern Tibet) and probably *G. s. yarcandensis* Blanf., 1875 (Kashgar) enjoy importance as independent forms. (V.H.)

Biology

Population. In the eastern Trans-Caucasus 5,750 goitered gazelle inhabited an area of about 8,000 km^2 in 1937; this population in 1940 numbered 5,500 to 6,000 animals (Vereshchagin, 1939 and 1947).

There is almost no information on the population of goitered gazelle in Middle Asia and Kazakhstan. In December, 1954 between the Aral Sea and Balkhash aerial surveys established a population density of 0.001 to 0.5 per km^2. The total population of goitered gazelle throughout the territory of the survey was 2,700 animals. However, at that time most had congregated in a more southern region, in the Pri-Chuisk Muyunkum and Kyzylkum (Rakov, 1957). In central Turkmenia the population density of goitered gazelle in the early 1930's went up to 2.0 to 4.3 animals per km length of area surveyed on foot (Laptev, 1936). In Badkhyz in the 1940's the total population of goitered gazelle was around 2,000 animals and the population density 1.6 to 6.0 animals per km length of area surveyed on foot (Heptner, 1956). Some tens of thousands of animals lived throughout Turkmenia. A few hundreds of thousands probably lived throughout Middle Asia and Kazakhstan.

Habitat. Goitered gazelle prefer plains or gently rolling or terraced deserts with firm soils. Along mountain trails and rocky valleys with a gentle relief, mainly in spring, they may ascend mountains to heights of 2,000 to 3,000 m in Kazakhstan and Mongolia and up to 3,000 to 3,500 m in the Nan'shan (China). They avoid extensive sand massifs in summer but are found in sands in winter, especially during snowstorms.

They prefer semishrub halophytic deserts and grass-halophytic semideserts. They are extremely common in shrub deserts, including sparse saxauls, but found only in the periphery of saxaul forests in summer and deep inside forests only in winter.

430 Goitered gazelle inhabit extremely diverse types of vegetation and are found in nearly all types of deserts and semideserts within the range. They occur in almost lifeless rocky deserts where, apart from *Halogeton,* no other higher plant life appears, as well as in rich grassy and grass-sagebrush semideserts. Semishrub deserts of a different type are characterized by the presence of sagebrush, perennial halophytes, winterfat, and Russian thistle, commonly with ephemeroids and ephemeras such as onion, tulip, ferula, poppy, meadow grass, some species of brome grass, and others. The vegetative cover there is characterized by great complexity, patchiness, and low density; the yield of vegetative mass does not generally exceed two to three centners per hectare.

Food. The general list of plants consumed by goitered gazelle includes 35 to 40 species. In the eastern Trans-Caucasus some 15 plants are known to be consumed by this gazelle. Among them, in any case in spring, the main varieties are grassy ephemeroids and ephemeras; meadow grass is of utmost importance in the food ration of goitered gazelle (Vereshchagin, 1938). In Kazakhstan in summer gazelle prefer succulent caper and saltwort (*Anabasis* and *Salsola*), and feed more rarely on sagebrush, *Eurotia, Calligonum, Ephedra* and saxaul; they avidly consume the tops of muskmelon and succulent reed stalks as a source of moisture (Kostin, 1955). Bereznyak (1931) has reported that goitered gazelle in the Syugotin valley used to feed on sagebrush year-round, which is dubious. Goitered gazelle there visited fields and ate maize leaves (Derevyagin, 1947). In the foothills of the Dzhungarskii Alatau (Antipin, 1941) the main summer food plants for goitered gazelle were fescue, feather grass, spirea, *Galium,* onions, barnyard grass (*Anabasis*), *Atrophaxis,* and reeds; in winter saxaul was avidly consumed. On Barsa-Kel'mes Island 35 species of plants are known to be consumed by these animals. In spring of utmost importance are grasses (meadow grass, *mortuk,* brome grass and feather grass), ferula, and *Jurinea*; in summer *Aristida, Agropyron, Ephedra, Kochia,* and Siberian pea shrub; in autumn saltworts (barnyard grass and *Camphorosma*), and especially *Kochia;* and in winter barnyard grass, *Atrophaxis,* and *Aristida* (Vasenko, 1950). In the Bet-Pak-Dala 17 plants are consumed by goitered gazelle (Sokolov and Suvorov, 1955). Of them, spiranthea, *Hulthemia, Kochia* and camel's thorn (*Alhagi*) are of utmost importance in July and August; in September, in addition to the foregoing plants, goitered gazelle consume large quantities of saltworts (*Salsola*); and in October and November saltworts, sagebrush, and *Ephedra.* In the Kyzylkum the stomach contents of goitered gazelle contained 23 plant species (Mambetzhumaev, 1955). In spring the main food is represented by grasses and *Calligonum;* in autumn and winter saltworts (swampy) and *Peganum* predominate. In the southern Ustyurt and Mangyshlak (Minervin, 1944 and 1955), goitered gazelle, assured of drinking water because of proximity to the sea, consume in summer mainly lichens *Thelaschistis lacunosus* (75% of stomach contents) and a small amount of leaves and fruits of buckthorn (10 to 15%) and *Ungeria* bulbs. On the sea coast goitered gazelle also gather fresh algae, which evidently serve as a source of water. In arid zones they do not touch dry lichens but gather succulent capers. Camel's thorn, tamarisk, and barnyard grass have been found in stomach contents as food supplements. In Badkhyz in summer these gazelle also feed on the most succulent plants (saltwort and sagebrush); quite often stomach contents have contained almost exclusively pistachio fruits and leaves. On hot days in the Murgab valley they graze on green cotton fields. Outside the droughty period, meadow grass forms the most important constituent in the diet of Badkhyz goitered gazelle (Heptner, 1956). In Mongolia the stomach contents of gazelles caught from June to August contained no less than 17 plant species, among which the main constituents were feather grass, onion, *Halogeton*, barnyard grass, and *Peganum*; next came *Ephedra*, berries of *Nitraria*, and various saltworts (Bannikov, 1951 and 1954).

Thus, the main summer food of goitered gazelle everywhere are the more succulent varieties, most often saltworts, capers, pistachio, and others. The choice of summer food is determined mainly by the 431 moisture content of the plants and not their edibility. When goitered gazelle remain close to open water sources, they may feed even on dry food such as grasses and lichens. Outside the period of drought, grasses, forbs, and saltworts are extremely important dietary items.

The weight of the stomach contents of goitered gazelle varies from 2.7 to 3.5 kg, which represents 10.5 to 15.9% of body weight. In one day a gazelle eats roughly 6.0 kg of green feed, i.e., about 30% of its body weight (Heptner, 1956).

For much of the year Middle Asian goitered gazelle are quite satisfied with the moisture contained in green plants. At the end of spring, depending on pasture desiccation, these gazelle wander in search of more succulent foods (for example in the foothills) and select plants with a high moisture content. Occasionally, but never daily, they drink water. In summer, in the period of utmost aridity (June to August), most of the animals move to pastures located close to springs and creeks, and regularly visit water sources. Only a few animals remain in waterless deserts where they feed very selectively on the most succulent plants (Minervin, 1944 and 1955; Heptner, 1950 and 1956). Nursing females, for whom water loss is particularly high, are the first to migrate toward water sources in southern Turkmenia, commencing movement even from the end of May (Heptner, 1956).

In Central Asia, where spring is the driest period of the year and rains, usually localized, are frequent in summer, goitered gazelle do not experience much water shortage and, by extensive wandering, invariably find pastures with succulent food. They visit water sources from time to time, more often in spring than in summer (Bannikov, 1951 and 1954).

En route to water-holes goitered gazelle will take up to three to seven days to travel a distance of 10 to 15 km. They usually approach water sources leisurely, grazing along the way. Movement occurs at dusk, during the night, early morning, and rarely during the day. They prefer water sources with open flat banks and avoid drinking at places where shrubs and dense reeds obstruct entry. They approach water singly or in small groups. They prefer fresh water but will lap brackish water, and even sea water. In the dry, warm

Fig. 137. Spring in Bet-Pak-Dala serving as a water source for goitered gazelle. Photograph by A.G. Bannikov.

season their daily water intake amounts to three to four liters (Minervin, 1944 and 1955; Heptner, 1950 and 1956; Flerov, 1935).

Home range. Data on the home range size of goitered gazelle are almost nil. Living in small groups or herds, these animals often perform significant migrations over distances of some hundreds of 432 kilometers (see below). Excluding such wanderings and the event of escaping winter, goitered gazelle usually cover 10 to 15 km per day. In summer, excluding movements to water holes when gazelle cover 15 to 30 km a day, their daily movement usually constitutes only a few kilometers. Thus the winter territory of a group of goitered gazelle comprises several hundred square kilometers and the summer territory less than a hundred square kilometers.

Daily activity and behavior. In winter goitered gazelle graze throughout the day, sometimes with a small break at midday. They spend the night in beds located most often in lowlands. In summer a distinct break in the daily feeding cycle occurs during the hottest hours, extending from 9:00–10:00 a.m. to 4:00–5:00 p.m. By spending the hottest part of the day resting in shelters, the animals economize on water. Goitered gazelle also spend much of the night bedded down.

Beds are most often situated on level ground. During the day gazelle prefer to lie in the shade of even a small bush. A single favorite bush may be surrounded by several beds as the animal shifts from one to another, following the shade as it moves around the bush. The animal keeps its head in the shade first and foremost. In pistachio plantations and in deserts where lone elms grow, goitered gazelle lie down in the shade of trees during the day.

Beds which have been used many times are in the form of an oval pit up to 70 to 90 cm long. At the end of it there is almost invariably a heap of dung. Beds are usually disposed singly, some dozens or more meters away from each other. At night goitered gazelle love to lie on smooth clay-surfaced deserts. During the day, whenever possible, they even lie under precipices. Sometimes, due to frequent usage, small niches form in such places in the cliff wall (Heptner, 1956; and others).

A goitered gazelle disturbed in its shelter breaks into a rapid run but, after running 200 to 300 m, it usually stops to assess the danger. Following this, it moves off in a trot, most often making a broad circle. Like other ungulates of open expanses goitered gazelle also attempt to cut back across the pursuer's course.

The stride of a goitered gazelle is 55 to 88 cm, lengthening on trotting to 44 to 128 cm, and increasing up to 310 to 574 cm in a gallop. The speed of running is 55 to 62 km an hour (Mambetzhumaev, 1955). The cardiac index of males is 6.56 to 8.37, females 9.31 to 10.0, and juveniles 9.04 to 11.59 (Heptner, 1956).

The sense of hearing is extremely well developed in goitered gazelle, vision poor, and the sense of smell poorer still.

There are two distinct periods in the year when herd size differs sharply: 1) the spring–summer period when goitered gazelle live singly or in small groups of two, three, or five animals; and 2) autumn-winter period when they live in herds of several dozen to hundreds of animals. In winter, i.e., January–February, gazelle herds are maximum in size. On the average a herd consists of several dozen animals. However, in regions where the population of animals is high individual herds of several hundred animals may form.

These evidently represent a temporary union of smaller herds in particularly favorable grazing grounds.

Winter herds begin to dwindle from the middle of March to April. Gestating females are the first to abandon the herd, moving singly or more rarely in groups of two or three. Somewhat later, generally toward the end of April and in May, males and barren females also separate from the herd and live in groups of seven to nine to twelve animals each. At the end of May to June these groups on moving to summer pastures usually break up and single animals or groups of two, three, or four animals predominate. Thus, throughout summer only females with one or two fawns or single males or small groups consisting of males, barren females, and yearlings are seen.

From the end of August to September females and juveniles begin
433 to form herds of 10 to 30 or more animals. Adult males also begin to attach themselves to herds or move in groups of three to five to nine animals. In the middle or at the end of September young begin to separate from females. Adult males then split female herds, each male taking away a group of two to three to five females which he protects from rivals. At the end of rut, usually in December, males separate from females and move separately in small groups. Females, however, join the young and form large winter herds of several dozen to hundreds of animals. Males usually join these herds by January. This period of maximum gregariousness extends up to spring (Kostin, 1955; Bannikov, 1954; Heptner, 1956; Sludskii, 1956; and others).

Seasonal migrations and transgressions. In much of the range goitered gazelle undertake seasonal migrations. Autumn-winter-spring migrations are distinct, mainly in the northern parts of the range, and associated with snowfall. Summer migrations are characteristic of much of the population and determined by the conditions of water sources and grazing grounds.

In autumn, with snowfalls and impoverishment of grazing grounds, goitered gazelle move away from the Pri-Balkhash into the foothills of the Dzhungarskii Alatau where snow is blown off the gentle southern slopes and thaws rapidly (Derevyagin, 1947). A similar phenomenon also occurs in the Syugotin valley, whence goitered gazelle move into the foothills of Bol'shoi and Malyi Boguta to winter (Zverev and Keleinikov, 1947).

In the plains of Kazakhstan and Middle Asia, i.e., in Mangyshlak, the northern Pri-Aral, and Bet-Pak-Dala, most goitered gazelle migrate south with the commencement of snowfalls so that the majority of wintering animals are seen south of the Chu and

Syr-Darya rivers. However, winter movements in the Ustyurt, especially along the Sary Su River, are rather poorly defined; in mild winters, along the Sary Su goitered gazelle are seen north to Kyzyldzhar (Sludskii, 1953; Kostin, 1955; Mambetzhumaev, 1955). There are no perceptible migrations of goitered gazelle in Turkmenia, Trans-Caucasus, and Central Asia in normal years because of the absence of snow or a negligible snow cover (Gromov, 1937; Vereshchagin, 1938; Bannikov, 1954; Heptner, 1956).

Periods of autumn and spring return migrations are extremely variable and depend on the place, and on the conditions actually prevailing in a given year. The first to move out from the Pri-Balkhash, even in September, are juveniles; older animals migrate at the end of October or early November.[75] Return migrations from the winter pastures occur at the end of February (Derevyagin, 1947). In the Syugotin valley autumn migrations take place in mid-November; gazelle leave wintering sites at the end of February (Zverev and Keleinikov, 1947). In the plains of Kazakhstan migrations south occur in October and November and return journeys in early March (Kostin, 1955).

Summer migrations represent a displacement of the majority of the animals. Due to the desiccation of desert plants gazelle move into more succulent pasture grounds or close to watering places. The site of summer congregation of goitered gazelle is a pasture ground within 10 to 15 km of water sources. This phenomenon is distinct, for example, in the southeastern Karakum, whence the animals gather together on the shore at Murgab, Kushka and Tedzhensk at the end of June or July; mothers with sucklings are the first to be seen in summer on the Murgab grazing grounds, followed by old males. In southern Mangyshlak and Ustyurt goitered gazelle congregate close to the shores of the Caspian Sea (Heptner, 1956; Minervin, 1955; Mambetzhumaev, 1955). In other regions of southern Turkmenia and Kazakhstan most gazelle move in summer into the foothills where the pasture is more succulent and springs are available (Laptev, 1934; E. Strautman, 1953; Minervin, 1955; and others). In Central Asian deserts migrations, like those of gazelle seen elsewhere in Middle Asia, occur only in years of summer drought. Furthermore the animals congregate more often not by rivers or lakes but in the foothills (Bannikov, 1954).

434 Sporadic migrations of goitered gazelle under conditions of natural calamities have not been adequately studied. They occur most often during unusual snowfalls or when the ground is ice-crusted

---

[75] According to A.A. Sludskii they all migrate together.

(Shnarevich, 1952; Sludskii, 1953; Mambetzhumaev, 1955; and others). Goitered gazelle do not like snow and attempt to leave regions with a high snow cover. Evidently, unlike saiga, goitered gazelle are incapable of prolonged migrations over long distances, and perish in large numbers (see below). Sporadic migrations may be induced by drought, steppe fires, and other natural calamities. In southern Turkmenia where the grass is very dense and grows taller in some years (mainly meadow grass), major fires occurred even before the 1940's which denuded several thousands of hectares. In such situations goitered gazelle desert large expanses (Heptner, 1956).

Reproduction. In the eastern Trans-Caucasus goitered gazelle become sexually active from November to the first half of December (Vereshchagin, 1938). In western and central Kazakhstan the rut commences in the first half of November to early December (Kostin, 1955; Afanas'ev and Sludskii, 1947; Derevyagin, 1947; Shnarevich, 1952; Ismagilov, 1954; Sludskii, 1956). In eastern Kazakhstan rut occurs from the end of November or in December (Sludskii, 1956). In southern Kyzylkum it commences in the latter half of November and extends up to mid-December (Mambetzhumaev, 1955). In Turkmenia and Tadzhikistan rut occurs in October and November (Heptner, 1956), and in Mongolia from the first half of December through January (Bannikov, 1951 and 1954).

Thus, in the southwestern part of the range rut commences a month earlier than in Kazakhstan, and in the east a month later. Periods of rut may shift either way, depending on the conditions prevailing in a given year. In years of drought rut sets in a week or two later (Sludskii, 1956). Much later periods of rut and hence delayed fawning in Central Asian deserts are evidently determined by late vegetation associated with dry springs.

The period of rut itself is preceded by fights among males and the assumption of "rut behavior" from mid-September. In this period a sharp increase in the secretory functions of the inguinal and preorbital glands is apparent. "Rut behavior" in adult males is exhibited by digging small pits with the hooves of the forelegs in which the animal defecates. Another male finding such a pit, smells it, rakes up the old feces, and fills the pit with its own. Such pits are formed and visited only by adult males; they serve as marks of territorial occupation similar to marks made by dogs and many other animals on pillars and rocks (Antipin, 1941; Ismagilov, 1954; Sludskii, 1956).

Every adult male before the commencement of rut gathers around itself a herd of two to five females, moves with it, and protects it from rivals. At this time fights take place among males, which in rare cases may lead to death or mutilation of one or the other animal (Derevyagin, 1947; Dement'ev and Turov, 1951; Ismagilov, 1954; Sludskii, 1956). In the period of rut males feed little, become emaciated, fall prey to predators, or perish in the event of natural calamities (Vereshchagin, 1938; Derevyagin, 1947; Sludskii, 1953 and 1956).

Females usually come into estrus for the first time at the age of 18 to 19 months; exceptionally this may occur in the year of birth, i.e., at the age of 7 to 8 months (Heptner, 1956; Sludskii, 1956). Females reproducing for the first time mate one or two months later than those which have fawned in the previous year. This explains the prolonged period of rut in the population (Ismagilov, 1954). Males become sexually mature at the age of 18 or 19 months but usually do not mate because they are driven away from females by older and more powerful rivals. Thus males mate for the first time at the age of 2.5 years (Ismagilov, 1954; Sludskii, 1956).

The gestation period has not been accurately established but, judging from the periods of mass rut and the birth of young, it lasts about 5.5 to 6.0 months. Fawning is prolonged among goitered gazelle not only in the range as a whole, but also in a given population. In the Trans-Caucasus young arrive from early May to the end
435 of that month (Dyukov, 1930; Vereshchagin, 1938 and 1951). In Turkmenia births have been recorded in April and May (Belovnev, 1937; Dement'ev, 1954; Heptner, 1956) and in Tadzhikistan also in April and May (Flerov, 1935; Grim, 1937). In the southern Kyzylkum newborn goitered gazelles are seen in the first half and middle of May (Mambetzhumaev, 1955). In Kazakhstan, in the Ustyurt area, gazelles fawn from April to the first half of May or up to the end of May (Kostin, 1955). On Barsa-Kel'mes Island fawning occurs roughly around the same period but some stray fawns have been found in early June and even in the first few days of July (Ismagilov, 1954). In Bet-Pak-Dala fawning commences in early May, peaking in the middle or latter half of that month (Sludskii, 1956). In southeastern Kazakhstan fawning commences in the latter half of May and extends up to June (Antipin, 1941; Sludskii, 1956). In Mongolia goitered gazelle fawn from the end of June to early July (Bannikov, 1951 and 1954). Thus the earliest period of fawning, similar to the period of rut, occurs in the southwest and the latest in the eastern part of the range (a difference of 1.5 months). Delayed births in the eastern sector are determined by late vegetation in Central Asiatic deserts and cold and dry spring seasons which are unfavorable for fawns.

In the latter periods of gestation females usually remain aloof from males and move singly or in small groups of two or three animals. At that time they select a site for fawning. Immediately before birth of young they leave the group and give birth at a distance of several hundreds of meters or more from one another, there by avoiding the formation of dense gatherings or a "delivery room," common in the case of saiga (Antipin, 1941; Sludskii, 1956; and others). This is so at places where the total population and density of goitered gazelle is not high. In southern Turkmenia in periods of high gazelle population large gatherings of females at a "delivery area," reached from considerable distances, have been described (Radde and Val'ter, 1889; Heptner, 1956).

A level open section among sparse shrubs or a hollow, i.e., a site protected from cold winds, is selected for fawning. Quite often goitered gazelle fawn along borders of sandhills or along landslides and slopes in foothills. They avoid dense saxaul and other plantations, deep gorges, and narrow ravines. Newborn fawns usually lie on a bare plot of soil where they are camouflaged by their color. Usually birth sites are located no more than 10 km away from water holes (Severtsov, 1873; Antipin, 1941; Kostin, 1955; Ismagilov, 1954; Sludskii, 1956).

In Kazakhstan, given favorable conditions, an average of 75% of the females deliver twins, about 14% a single fawn, and 11% remain barren. Rare females (0.4%) have produced triplets (Antipin, 1941; Sludskii, 1956). In Turkmenia and Tadzhikistan twins are common and a single fawn very rare (Flerov, 1935; Grim, 1937; Balovnev, 1937; Heptner, 1956; and others). In the Trans-Caucasus, on the contrary, a single fawn is the rule (Vereshchagin, 1947; Dyukov, 1930). The same is true in Mongolia, where barrenness has been established as 12% (Bannikov, 1954).

Growth, development, and molt. A few hours after birth the fawn can stand on its legs and run a few meters. It is still very weak, however, and generally remains lying down for the first three or four days. In concealment the young animal gathers its legs under itself and extends its neck; rarely, it lies on its back with its head to one side. After five days it is capable of standing firmly and, with the approach of danger, jumps up and runs away for several hundred meters and again conceals itself. For two weeks fawns do not move with their mothers, but remain lying down most of the time, wandering occasionally only in the proximity of their beds.

Fawns suckle three times a day: early morning, usually at dawn, midday, and late evening. Having suckled her fawns for the last time, the female lies down to rest not far from them but some tens of meters away. During the day the mother wanders as much as several

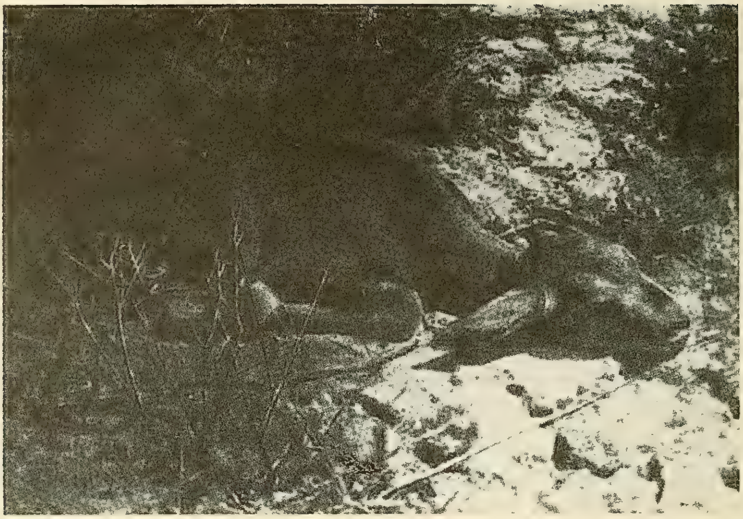


Fig. 138. Newborn goitered gazelle. Photograph by A.A. Sludskii.

436 kilometers. On returning to her fawns, the female exercises great caution, approaching the place of their shelter only after ensuring that no danger lurks nearby, and calls them with a soft moo. A goitered gazelle fawn consumes on the first day 15 to 30 g of milk at one time and later 300 to 500 g. The milk contains 39% fat (Ishunin, 1956).[76] The female protects her offspring from predatory birds and foxes with her forehooves and by butting; she attempts to divert man or wolf from her young.

The young begin to follow their mother at age two weeks or slightly later. They begin to nibble grass eight to ten days after birth. At one month of age vegetative food predominates and at two months most fawns take wholly to pasturage and begin to live independently of their mothers. Lactation extends over two months, females lactating until August in most regions. However, some fawns separate from their mothers even at the age of 1.0 to 1.5 months (Ismagilov, 1954; Antipin, 1941; Kostin, 1955; and others).

In southern Turkmenia (Badkhyz), contrarily, the young remain with their mother for a much longer period. Lone juveniles are either orphans, those left behind by mothers going to a watering place, and so forth (Heptner, 1956). According to the data of Sludskii (1956) lactation in goitered gazelle continues for six months and juveniles suckle until October.

---

[76] Such a high fat content is dubious; perhaps a printing error occurred (3.9% intended ?)—V.H.

Newborn gazelles on Barsa-Kel'mes Island (10 animals) weighed 2.0 to 3.2 kg, with an average of 2.4 kg; body length 49.0 to 59.0 cm, with an average of 54.3 cm (Ismagilov, 1954). In Bet-Pak-Dala (5 animals) newborns weighed 2.6 to 3.1 kg and body length was 55 to 58 cm (Sludskii, 1956). At one month of age the animals weighed 7.0 to 8.0 kg, at three months an average of 13.5 kg, and at six months males 17 to 20 kg. A goitered gazelle 1.5 years old weighed about 20 kg and its body length was 102 cm (Ismagilov, 1954; Sludskii, 1956). Incisors and [incisiform] canines (altogether four in each half of the lower jaw) are fully cut in newborn fawns; the middle (inner) one is particularly large and cut aslant inward.

In males horns are distinct at the age of one month, when their length is 10 to 15 mm, and by three months (measured along the curvature) reach about 60 mm. In 1.5-year-old males horn length (19
437 animals) varied from 8.5 to 30 cm, with an average of 17.3 cm; the number of rings on the horns reached 10 or 11 (Ismagilov, 1954; Sludskii, 1956). In Kazakhstan short spikes were found on 5.5% females and measured 2.5 to 5.0 cm in length (Sludskii, 1956).

The weight of adult males on Barsa-Kel'mes Island was 20 to 43 kg, with an average of 36 kg (15 animals); females weighed 18 to 28 kg, with an average of 24.2 kg (14 animals) (Ismagilov, 1954). In Bet-Pak-Dala males (10 animals) weighed 27.0 to 33.8 kg and females (58 animals) 21 to 33 kg. In the Ili River valley males in January (10 animals) weighed 20 to 28 kg and females (11 animals) 20 to 26 kg (Sludskii, 1956). Adult males of Badkhyz (4 animals) weighed 25.6 to 29.4 kg and females (4 animals) 18.0 to 20.4 kg (Heptner, 1956).

Longevity in nature is not known. Males not less than five or six years old are known and much older females have been reported. In captivity they live up to age eight or nine years.

Molt of goitered gazelle has not been studied thoroughly; evidently only a spring shedding of hair occurs. In the southern Kyzylkum spring molt commences in mid-March and ends in mid-May (Mambetzhumaev, 1955). In Bet-Pak-Dala goitered gazelle molt from mid-April to mid-May (A.A. Sludskii). At the end of April to early May molt ceases in Azerbaidzhan (Vereshchagin, 1938). Gazelle in Mongolia molt until the end of May (Bannikov, 1954). The first areas to molt in spring are the cheeks, ears, and almost simultaneously the speculum and tail. Later, molt extends from the cheek to the crown and covers the upper part of the neck, gradually descends to the sides, and runs along the back. From the speculum molt extends to the thighs and the distal portions of the hind legs. The sides molt next, while the last to molt are the undersurface of the trunk, chest, and abdomen (Mambetzhumaev, 1955). The autumn growth of wool commences on different dates in October and ceases by the end of November or early December.

Enemies, diseases, parasites, mortality, competitors, and population dynamics. The main enemy of goitered gazelle is the wolf. A particularly large number are killed by wolves in winters of abundant snow, which emaciated animals find difficult to negotiate. In Turkmenia goitered gazelle invariably fall prey to the cheetah (Heptner, 1956). Caracals hunt gazelle, especially their young. In the past, tigers waited for gazelle at water holes. Newborns were sometimes the quarry of foxes and golden eagles. Stray dogs also kill the young. Goitered gazelle remnants have been seen near nests of predatory birds such as steppe eagle, and griffon and other vultures, which probably feed on the carcasses of gazelle or kill weakened animals.

Eighteen species of worms are known to parasitize goitered gazelle in Kazakhstan (Sokolov and Boev, 1950) but their pathogenic importance is not known. All of the helminths found in these gazelle also parasitize farm animals (Sokolov, 1954). Goitered gazelle suffer intensely from two species of skin gadfly (*Pavlovskiata subgutturosae* and *Crivellia corinnae*), the larvae of which are quite often found on the "speculum" and may number from 15 to 180 (Grunin, 1949 and 1956; Kostin, 1955). Six species of ticks also parasitize goitered gazelle. The lice *Linognathus tibialis* and *Damalinia appendiculata* have also been found (Galuzo, 1953). In summer the animals often suffer from blood-sucking insects.

Saiga could be a competitor of goitered gazelle at some places.

Among natural calamities, those most fatal to goitered gazelle are deep snows and ice-covered ground. A snow cover 18 to 22 cm deep, especially when the ground is covered with crusted snow, is fatal to these animals (Vitovich, 1928; Sludskii, 1953). When snowfalls are intense, gazelle attempt to move away into snowfree regions; quite often they gather in the foothills where snow is blown away by winds and thaws rapidly (Vereshchagin, 1939; Shnarevich, 1952; Sludskii, 1953; and others). During the severely snowy winter of 1924 to 1925 goitered gazelle joined cattle herds in the Shirvan and Mil' steppes of the Trans-Caucasus (Golovin, 1925). In the Trans-Caucasus winters of excessive snow are recorded once every 15 to 20 years and the goitered gazelle population in such years falls sharply due to high mortality. The last severe winter, when many gazelles died in the Kur' lowlands, occurred in 1950.

438 In Kazakhstan high mortality among goitered gazelle has been recorded frequently: *dzhut* [continuous snow cover] in southeastern

Kazakhstan in 1945 to 1946, and in the south in the winter of 1950 to 1951 proved particularly fatal (Sludskii, 1953). In January, 1946 in Pri-Balkhash the snow cover at places was 50 cm deep, snow crust formed as a result of thaws, and goitered gazelle injured their legs severely. The animals were confined to shrub thickets along the Ili River and many could move only with difficulty. Goitered gazelle with injured legs were found under bushes of chingil, feeding on their thorny branches and pods. The weight of these adult animals was 10 kg less than normal. Weakened animals, primarily males, had been strangled by stray dogs. Mass attacks of epizootic diseases in February–March led to the death of several thousand goitered gazelle in the lowlands of the Ili (Evert, 1947). High losses of these animals as a result of ice crust formation were reported in Kzyl-Ordinsk district of Kazakhstan in 1938 and in western Mongolia in 1935. In Badkhyz severe snows in 1934 and 1957 (up to 40 cm) also resulted in the death of goitered gazelle (Ishunin and Korovin, 1948; Sukhinin, 1958).

The main factor responsible for a sharp drop in population of goitered gazelle is evidently winters of heavy snow and ice crust since gazelle are then unable to undertake distant migrations as do saiga. Following winters of *dzhut,* the population of goitered gazelle drops several times and the animals disappear altogether from some regions for quite some time.

Restoration of a goitered gazelle population proceeds far more slowly than in the case of saiga. This phenomenon is explained by the lower mobility of the gazelle, its lesser fertility, and its high mortality due to predators and man. During *dzhut* goitered gazelle invariably die in relatively greater numbers than saiga. For example, following winters with *dzhut* in 1945 and 1946 and in 1950 and 1951 in Kazakhstan, goitered gazelle disappeared from several regions and did not reappear until five to seven years later, while the saiga population was restored to its original number within two to three years (Sludskii, 1953 and 1955). Similar phenomena have been observed in the depression of the great western lakes of Mongolia, where gazelle disappeared after ice crust conditions in 1935 and were not restored for ten years, while saiga were restored within three or four years (Bannikov, 1951 and 1954). The fertility of goitered gazelles is such that the population can rise by 70 to 80% through birth of calves, given very favorable conditions, by autumn. In years following severe winters, however, only 50 to 55% of the population consisted of young by August (Sludskii, 1956).

Infant mortality among goitered gazelle is considerable, and may reach 40 to 50% by autumn (Sludskii, 1956; Heptner, 1956). The number of barren females, although low (8 to 12% of adults), is still two to three times greater than among saiga. The high mortality of young, relatively high barrenness, and relatively late sexual maturity (a year later than among saiga) are responsible for the slow restoration of gazelle populations. It is possible that an adverse role is contributed by the sex ratio disturbance in years following *dzhut*. In normal years the sex ratio among goitered gazelle is such that adult males comprise about 20% of the population; but in years after dzhut, during which the first to die are males, adult males constitute only 3.5 to 5.5% of the entire population (Sludskii, 1956).

Field characteristics. The relatively long black tail, rising vertically with fright, and distinctly visible against the background of the white speculum, makes it easy to differentiate goitered gazelle from Mongolian gazelle, which are very similar. The two species are often encountered at the same place. When resting quietly, the tail of the goitered gazelle hangs down. This species differs from saiga in its far more slender and elegant body build. While running, goitered gazelle execute broad jumps, raising their head or holding it level with the trunk, and not dropping it downward like saiga do.

The tracks of an adult goitered gazelle are about 55 to 60 mm long and 35 to 40 mm wide. They are heart-shaped, narrow, and long, with an extremely pointed end. A longitudinal hollow at the front end of the track is absent because the hooves are almost immo-
439 bile, even when resting on soft ground. The feces of goitered gazelle are in the form of small, dark pellets with pointed ends, measuring about 10 mm in length and 7.0 or 8.0 mm in thickness.

The beds of goitered gazelle are usually disposed under shrubs, tall grasses, and so on, and are in the form of circular or oval pits devoid of grass and absolutely free of rubble. Along the edge of the shelter a dung heap is invariably found. In winter gazelle lie on the bare ground after raking the snow with their hooves. Pathways to water holes are usually straight, without bends, and narrow. They are short in length and readily discernible, extending not more than 100 to 200 mm from the water.

In herds containing juveniles the soft bleats of fawns and delicate moos of mothers are distinguishable. In the period of rut males emit hoarse bellows. (A.B.)

Economic Importance

Goitered gazelle are extremely interesting objects of sport. In the past they constituted an important commercial species. Data on the number of gazelles caught are few since the animal was hunted mainly for its meat and hide, which were utilized by the hunters.

In the 1930's up to 2,000 goitered gazelle were caught annually in the Trans-Caucasus. In Middle Asia, especially in Turkmenia, some tens of thousands were caught annually. Historical evidence is available that Tamerlane's troops caught 40,000 goitered gazelle in one year (Kashkarov, 1936). More accurate information is available only for a few regions. In Semirech'ya in the 1880's about 400 animals were caught annually (Shostak, 1927). In the former Krasnovod district of the Zacaspiisk [Trans-Caspian] district in the 1890's about 600 goitered gazelle were caught annually (Silant'ev, 1898). These gazelle represented one of the main sources of meat for shepherds of southern Kazakhstan and particularly of Middle Asia. The total number of animals caught is not known but at some places averaged one or two per person per week. Recently the gazelle population has dropped steeply and measures for their conservation are urgently required.

In Tadzhikistan hunting of goitered gazelle has been totally prohibited since 1946, in Turkmenia since 1950, in Uzbekistan since 1950, in Kirgizia since 1952, and in Kazakhstan since 1951.

The most prevalent methods of hunting involved concealment at water holes and trapping the animals on their trails. Often the animals were chased. Goitered gazelle were hunted with the help of golden eagle, goshawk, and saker falcon [*Falco cherrug*]. The golden eagle copes well with a gazelle but hawk and saker falcon only restrain it until the arrival of the hunter. Sometimes hunting with birds was combined with Asian borzoi (tazy) [wolfhounds].

To catch goitered gazelle or saiga massive pens built of stones—"aran"—were used (see hunting of saiga), but proved less effective with gazelle since they rarely form large herds. In the 1930's hunting in automobiles was extensively practiced; the animal was chased during the day or shot at night when in the car headlights. This destructive method has been prohibited throughout the USSR.

The products obtained from goitered gazelle are high quality meat and hide. An average of 12 to 15 kg meat is obtained from one animal but an adult male can provide up to 18 kg. The hide is about 60 to 70 dm^2 and yields, after processing, a good quality chamois and box calf. Gazelle hide is commonly used for making bags for water and koumiss (fermented mare's milk). Such a bag is light, elastic, and without an unpleasant odor. More rarely, gazelle hide is used for making summer footwear.

Goitered gazelle sometimes damage cotton and other plantations, as well as crops. They also cause damage by eating saxaul shoots, inhibiting the regular growth of this most valuable desert tree. In autumn and spring they may compete with sheep in pastures as an exception. On the whole, the adverse effect of goitered gazelle is negligible.

In captivity goitered gazelle become domesticated quickly and are characterized by a gentle disposition. They reproduce well in captivity but do not survive for long. In 1929 nine goitered gazelle were acclimatized on Barsa-Kel'mes Island (Aral Sea) and by 1947 their population there was 2,300. Following the severe winter of 440 1948 to 1949 only 48 animals survived, and population growth as of 1958 has been minimal (Sokolov, 1958).

The goitered gazelle population has declined throughout its range. The main reason for this decline is unrestrained poaching. Year-round conservation is required for this valuable game animal. (A.B.)

Genus of Dzeren, or Mongolian Antelope [Gazelle]

Genus *Procapra* Hodgson, 1846

1846. *Procapra.* Hodgson. *Journ. As. Soc. Bengal,* vol. 15, p. 334. *Procapra picticaudata* Hodgson. 1918. *Prodorcas.* Pocock. *Ann. Mag. Nat. Hist.,* vol, 2, p. 130. *Antilope gutturosa* Pall. (V.H.)

Size, large or medium.

Lateral hooflets (of digits II and V) present; hooves of middle digits normally developed.

Facial part of skull slightly elongated and relatively massive; anteronasal profile somewhat swollen. Preorbital depression on lacrimals absent or very slight. Ethmoid pit present. Nasals slightly elongated without notches in anterior region and pointed and wedge-shaped. Premaxillae normally developed, their ascending processes usually reaching nasals. Tympanic bulla small.

Dental formula:

$$i\frac{0}{3},\ c\frac{0}{1},\ pm\frac{3}{3},\ m\frac{3}{3} = 32.$$

Appearance of $pm\frac{1}{}$ sometimes delayed and formula then:

$$i\frac{0}{3},\ c\frac{0}{1},\ pm\frac{2}{3},\ m\frac{3}{3} = 30.$$

Molars brachyodont.

In general horns as in *Gazella,* but usually shorter in length.

Muzzle not long and covered with hair except for a narrow vertical patch from lips to nostrils. Preorbital glands either absent or very poorly developed, like the carpal glands; inguinal glands absent in one species but present in another (*P. gutturosa*). Hoof glands poorly developed and their opening very small. Glands present behind horns. Tail short.

Color sandy, usually with a fairly large white speculum. Dark- and light-colored bands on flanks and facial pattern absent. Sexual dimorphism in coloration likewise absent. Females hornless. Teats two.

Behavior that of typical gazelle.

Procapra are inhabitants of steppes, often of semideserts and deserts, and high-altitude desert uplands.

The geographic range of the genus is confined to Central Asia and covers the Mongolian Republic in the north to the southern Altai and Trans-Baikal, northwestern, central, and western parts of northeastern China, Inner Mongolia, Ordos, Kansu, northern Szechwan and Tibet, and south to Ladakh, Kumaon, and Sikkim; western Kashgaria (?).

Genus *Procapra* is very close to genus *Gazella* and probably should be considered a subgenus of the latter. The link between these two groups is *G. subgutturosa,* the only species of genus *Gazella* in which the females are also hornless. On the other hand, reduction in skin glands, so characteristic of *Gazella,* occurs gradually in *Procapra*: in one species (*P. gutturosa*) some of these glands are still developed in a form approaching *Gazella,* but totally or largely reduced in the other two. From purely systematic and geographic considerations, *Procapra* represents a genus derived from *Gazella.*

441 The view that *Procapra* is closely related to *Pantholops* (orongo, chiru) is based on the known tendency toward reduction of $\mathrm{pm}\frac{1}{}$ in one species of *Procapra* (*P. picticaudata*) which is hardly a serious basis. Genus *Pantholops* is highly unusual and belongs to another subfamily (Caprinae).

Genus *Procapra* is known only from Pleistocene formations in Asia. In origin it is evidently associated with *Gazella*; it flourished in the region of the latter's present-day distribution and arose not earlier than the Upper Pliocene.

Three species have been described in genus *Procapra*: *P. picticaudata, P. gutturosa,* and *P. przevalskii.* Recently these were reduced to two by relegating *P. przevalskii* to a subspecies of *P. picticaudata*. Based on some differences between *gutturosa* and *P. picticaudata* in glandular development, *P. gutturosa* has been isolated in a special genus, *Prodorcas.* Some taxonomists consider this a subgenus but there is no adequate justification for such classification.

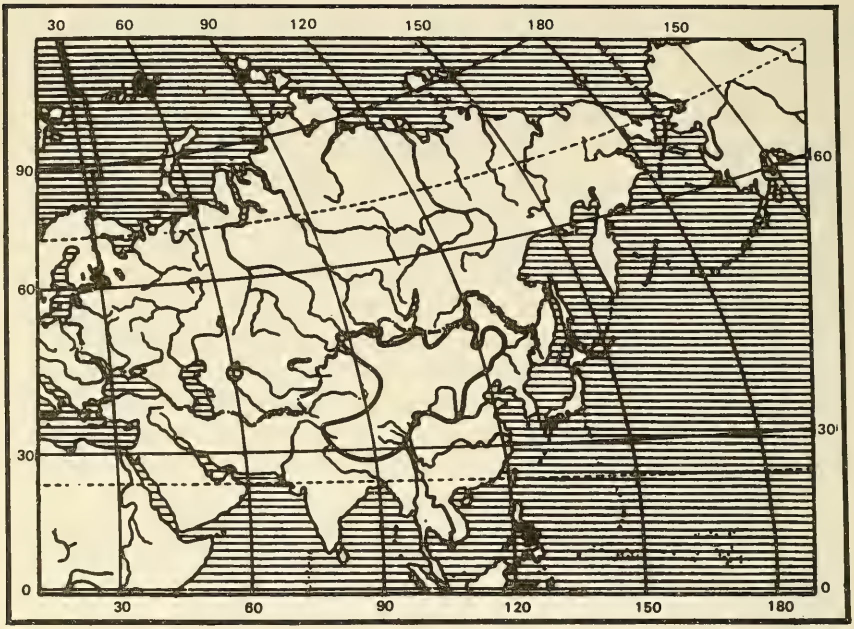


Fig. 139. Geographic range of Mongolian gazelle, *Procapra* Hodgs. V.G. Heptner.

There are two species in genus *Procapra*: *P. gutturosa* Pallas, 1777 and *P. picticaudata* Hodgson, 1846; these represent 6% of the present-day species of the subfamily.

These are game animals, mainly objects of sport.

In the Soviet Union one species is found, the Mongolian gazelle *P. gutturosa* Pallas, 1777, constituting 50% of the species of the genus and 0.3% of species of Russian fauna.

P. gutturosa is an inhabitant of the Trans-Baikal steppes and high-altitude steppes of the southern Altai. It is a game animal. (V.H.)

12. MONGOLIAN GAZELLE, OR DZEREN[77]

Procapra gutturosa **Pallas, 1777**

1777. *Antilope gutturosa.* Pallas. *Spicil. Zool.*, no. 12, p. 46, tab. 2. Upper course of Onon, eastern Trans-Baikal. 443

---

[77] "Dzeren" in Russian is a variation of the Mongolian name "zeer". Mongolians more often call it "tsagan zeer" (white dzeren). In Trans-Baikal it is often called "zeren'" and in Altai "eren'" or simply "steppe goat".

1777. *Antilope orientalis.* Erxleben. *Syst. Regini Anim.*, p. 288. substitute for *Antilope gutturosa* Pallas.

1913. *Procapra altaica.* Hollister. *Smiths. Misc. coll.*, vol. 60, no. 19, 1. Suok plateau at Bayan-Tsagan pass, Mongolian Altai. (V.H.)

Diagnosis

This is the only species of genus *Procapra* found in the Soviet Union.

Description

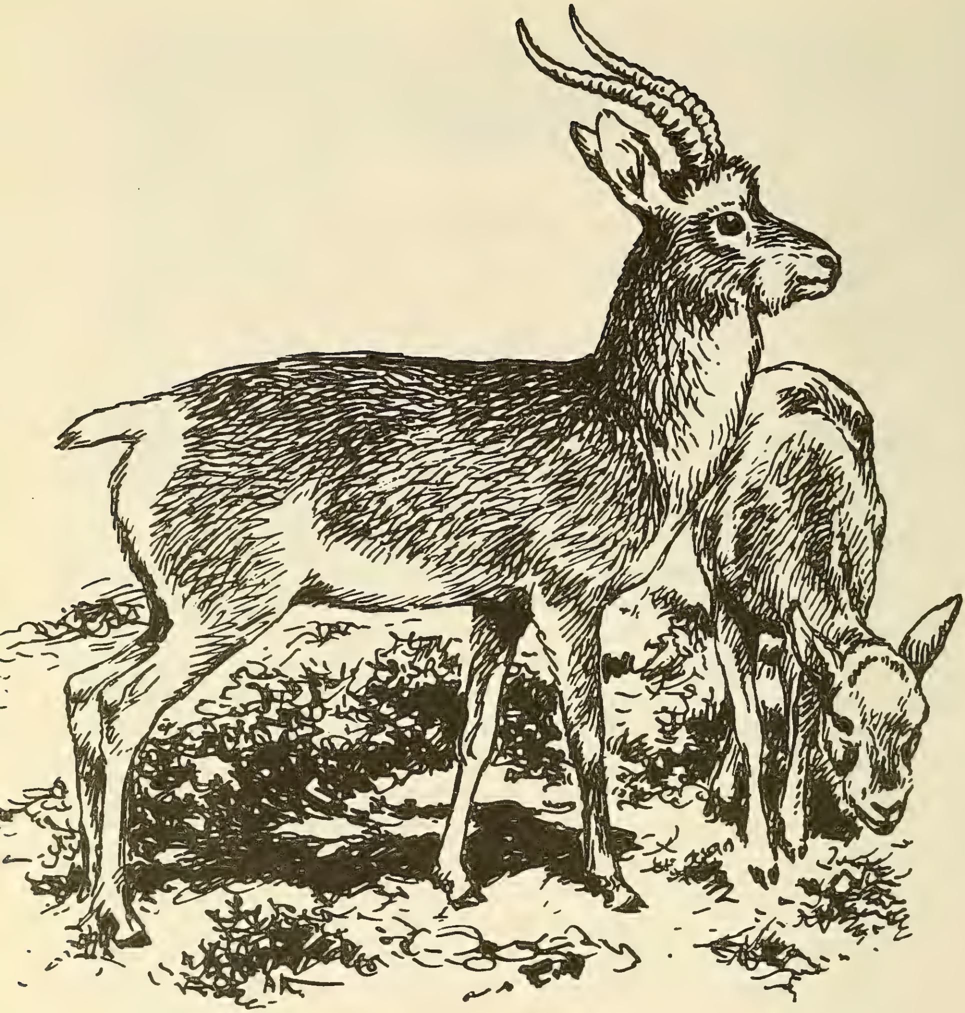
Antelopes of stout but elegant build standing on thin, slender, and strong legs. Back and chest broad. Withers slightly higher or equal to height of sacrum. Trunk roughly as long as height at withers. On neck of males an intensely developed larynx projects downward in the form of a goiter. Head large, broad, with large, S-shaped nostrils. Between lower corners of nostrils and along midline of upper lip, there occurs a narrow strip of bare skin. Eyes not very large but protruding. Irises dark brown or almost black. Lacrimal fossa small, covered with hair. Ears moderate in length and covered outwardly with light-colored hair; three indistinct furrows occur on their inner surface. Tail shorter than ears, bare ventrally, and covered with long light-colored hair dorsally, which is sometimes brownish at the tip.

Horns dark gray or oily black. Lower two-thirds of horn with thickenings in the form of rings; up to 24 to 26 (more often 16 to 18) such rings present in adults. Last 4.0 to 6.0 cm of horns smooth and round. In basal portion of horns rings oval in section. Horns lyrate, close-set at base, diverge gradually, turn back and inward in the upper portion, but not forward as in goitered gazelle; distance between horn tips 6 to 10 times greater than between their bases. Females do not sport horns.

Hooves black, fairly broad but pointed forward; width 1.5 times less than length. Hoof length 42 to 54 mm. Forehooves slightly (2.0 to 5.0%) larger than hind ones. Lateral hooves 12 to 15 mm long.

Winter hair long, up to 30 to 50 mm, and slightly curly. Coat on forehead, crown, ears, throat, and rear of back remarkably long and luxuriant. Long rigid hairs along sides of upper lip form whiskers. Winter color of upper body light sandy-gray, gradually running into white underside without sharp boundaries. Outer surface of ears, nose, forehead, and upper part of cheek light or dirty yellowish-gray.

Summer hair 15 to 25 mm long and yellowish-sandy in upper



442 Fig. 140. Mongolian gazelle, *Procapra gutturosa* Pall. Sketch by A.N. Komarov.

portion; abdomen and chest white with dirty yellow tinge. Lower lip, anterior portion of upper lip, throat, inner surface of legs, and speculum white, sometimes with a yellowish or grayish tinge. Top and sides of speculum stand out sharply from sandy color of back but yellowish-rusty patches absent along borders. Coloration of back, sides, and foresurface of lower third of legs more intense. Darkening in extreme lower part of anterior surface of legs between middle and lateral digits absent. Upper part of muzzle pale brownish-gray; crown, occiput, and sides of neck rusty shade; down the neck up to the chest yellowish-white. Sexual dimorphism in coloration not discernible.

Measurements: Body length of males (n = 56) 105 to 148 cm and females (n = 41) 110 to 121 cm; height at withers in males 62 to 84 cm, and females 54 to 74 cm; tail 9 to 12 cm; ears 9.5 to 12 cm; length of horns along curvature 180 to 280 mm; and horn diameter at base 32 to 40 mm (longitudinal) and 22 to 33 mm (transverse). Males (n = 87) weigh 24 to 39 kg, and females (n = 64) 20 to 28 kg. Maximum length of skull in males 236 to 263 mm, and in females 222 to 251 mm. For skull characteristics, see description of the genus. (A.B.)

444 Taxonomy

Compared with other species of this genus, *P. gutturosa* is a more specialized form, revealed notably in gland development. (A.B.)

Geographic Distribution

This species inhabits the steppes and semideserts of the Mongolian Peoples' Republic, Inner Mongolia, northeastern part of Kansu (China), southwestern Altai (Chuya steppe), southern Tuva region, and eastern Trans-Baikal.

Geographic Range in the Soviet Union

The reconstructed range in the Soviet Union covers Chuya steppe in the southwestern part of the Russian Altai into which Mongolian gazelle penetrated from Mongolia through the Sailyugem range. In the south they reached the slopes of southern Chuya mountain range, in the north the Kurai range, and in the west along Chuya River valley evidently up to the Kurai steppe (Gebler, 1837; Demidov, 1900; Sapozhnikov, 1911; Hollister,1913). In the 1930's these gazelle were still common in the western part of Chuya steppe and along the Chagan-Burgazi River as far as Sailyugem range (Bulavin, 1934; Kolosov, 1939). At present this species is a rarity in the Chuya steppe. In 1956 and 1957 herds of five or six animals were sighted between Kosh-Agach and the Mongolian border (P.P. Tarasov).

Within the Tuva region Mongolian gazelle were common south of the Tannu-Ola range, especially in the basin of Lake Ubsu-Nur (Grum-Grzhimailo, 1914; Polikevich, 1923). A large number of these gazelle were seen on the Tes-Khem River in the winter of 1935. In the 1940's they survived only in the basin of Ubsu-Nur and were rarely seen, mainly in winter, on the Tes-Khem River (Yanushevich, 1952). In recent decades Mongolian gazelle have not been reported in the Tuva region.

In western Trans-Baikal there was evidently no permanent residence of Mongolian gazelle, but they penetrated now and then from Mongolia along the Selenga River in winter. The last find was reported in the winter of 1947 to 1948, when several dozen were seen around Ust-Kyakhta village and one gazelle killed. A lone animal had been seen in the winter of 1922 (Leont'ev, 1949).

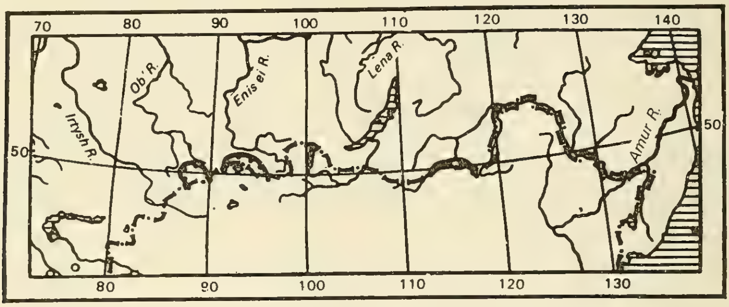


Fig. 141. Reconstructed geographic range of Mongolian gazelle, *Procapra gutturosa* Pall. in the USSR. A.G. Bannikov.

In eastern Trans-Baikal Mongolian gazelle were more regular in the past but not sighted every winter. From southern Mongolia and Barga they penetrated north up to the right bank of the Onon and in the eighteenth century were reported on its upper reaches (Pallas, 1777). In the nineteenth century they were common in some winters on the left bank of the Argun, reaching there up to the Onon (Radde, 1862). Later, in eastern Trans-Baikal, Mongolian gazelles occurred rarely in the Kailastui and Tsurukhaitui regions on the Argun River, but were common on Lakes Zun-Torei and Barun-Torei the south and southwest of the Borzya River (Kirilov, 1902; and others). In the 1940's Mongolian gazelle extended north to a line running through the northern slopes of the Chir-Abagatui mountains (Argun range), Nikolai-Torm Pad', the vicinity of Berezovaya *griva,* Matsiev station, Lake Chindant, Fedkin ford on the Borzya
445 River, and around Kulusutai and Bain-Tsagan villages (Fetisov and Khrustselevskii, 1948). The last finds of large numbers of Mongolian gazelle in eastern Trans-Baikal occurred in 1925 to 1926 and 1944 to 1945. Some individual animals and groups used to remain in eastern Trans-Baikal even in summer; they were known by a special name—"ostal'tsy" ["those remaining"] (Cherkasov, 1867). In recent years Mongolian gazelle have been a summer rarity in Trans-Baikal (Pavlov, 1949).

Mongolian gazelle are presently found in small numbers almost every year in spring (April and May) or in autumn (September) within eastern Trans-Baikal, close to the state boundary with Mongolia and China. More often they occur in the region of Durbach station (40 km from Borzya station toward Solov'ev station) at Lake Chindant. Early in the spring of 1957 about 100 were seen and in May, 1958 a group of four to six (A.N. Leont'ev). In September, 1958 groups of 8 to 12 were sighted on the western bank of Lake Borun-Torei; in the same month but more southward and closer to the boundary a herd of 200 to 300 animals was reported.

Geographic Range outside the Soviet Union

The northernmost point of the present habitation of Mongolian gazelle is the northwestern corner of the range, which falls in Mongolia in the basin of Lake Ubsu-Nur, i.e., roughly 50° N lat. and 91° E long. From there the northern boundary runs to the forestless slopes of the Khankhukhei range and farther on approaches the Khangai. Bypassing the Khangai on the south, the range boundary again rises along the steppe valleys of the Orkhon River and its right tributaries almost up to 49° N lat. Farther away the boundary again descends and encircles the Khentei from the south, approaches the Ul'dzya River, and extends east to Barga (northeastern China).

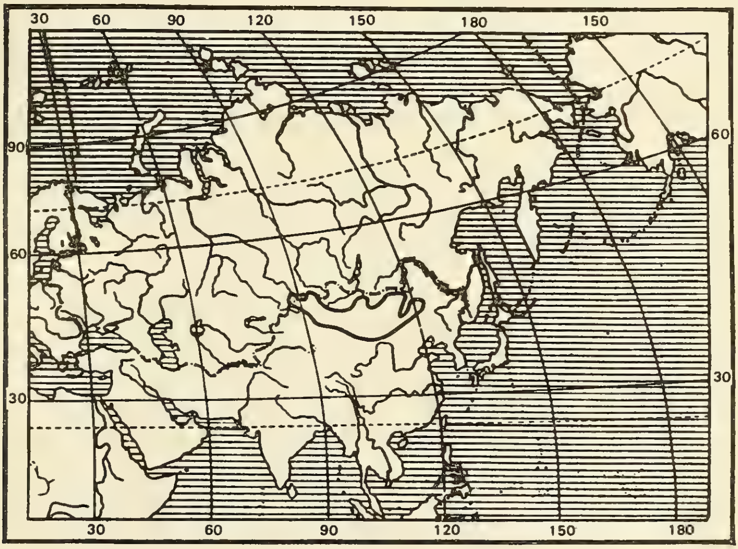


Fig. 142. Reconstructed geographic range of Mongolian gazelle, *Procapra gutturosa* Pall. A.G. Bannikov.

Sharply descending along Great Khingan and encircling it from the south, Mongolian gazelle penetrate the southern extremities of the Sunlyao plains but do not reach nowadays to the Nonni and Sungari Rivers, nor even to Harbin where they were common even in the 1920's (Lukashkin, 1927). Mongolian gazelle penetrate northward here no farther than 45° N lat. The eastern boundary of the range crosses the midcourse of the Liao Ho River somewhere. In the south, the Peking plains fell within the range in the last century and the beginning of the present. Nowadays the animals do not penetrate beyond the Great Wall. With the spread of agriculture in Inner Mongolia, the range boundary of Mongolian gazelle withdrew in
446 the northwest. The southern boundary, evidently, does not cross the Hwang Ho River, but rises toward Solon-Khere and the Gurban-Saikhan range in Mongolia. The southernmost point of habitation of the species lies roughly at the intersection of 41° N lat. and 112° E long.[78] Along the foothills of the Gobi and Mongolian Altai and the intermontane depressions, the boundary for Mongolian gazelle rises toward the Sailyugem range, the Kharkhin group of mountains, and farther away, the basin of Lake Ubsu-Nur. The southern and northern boundaries are highly unstable and vary according to the thickness of snow cover and state of pasture. Within these boundaries Mongolian gazelle are absent in elevated sections with a preponderance of rocks, high mountain steppes, and forest groves. They are also absent in saline desert basins. (A.B.)

Geographic Variation

This species does not give rise to distinct geographic forms. Animals from the Mongolian Altai are indistinguishable from those from eastern Mongolia and hence the form *altaica* described from Bayan-Tsagan-Gol (Hollister, 1913) cannot be accepted. (A.B.)

Biology

Population. In the last century herds comprising many thousands of Mongolian gazelle wandered in some winters into eastern Trans-Baikal, but in summer only a few remained (Radde, 1862; Cherkasov, 1867). When last found, Mongolian gazelle were several thousand strong in eastern Trans-Baikal in the winters of 1925 to 1926 and 1944 to 1945. At present, several dozen, more rarely several hundred, are found in eastern Trans-Baikal. In western Trans-Baikal a very small number were counted in 1922. Some lone animals penetrated the Soviet Union and several dozen were sighted in the winter of 1947 to 1948 (Leont'ev, 1949).

---

[78] References to the Mongolian gazelle reaching Lake Kukunor (Przewalski, 1883) pertain to another species, *P. picticaudata*. Similarly erroneous are references to Mongolian gazelle inhabiting the Ching Shan and Szechwan, and even Tibet, and reaching southward to Ladakh and Sikkim (Sokolov, 1959).

Several hundred of these animals used to be seen in winter in the Tuva district along the Tes-Khem River and in the basin of Lake Ubsu-Nur; in summer the numbers fell sharply (Polikevich, 1923; Yanushevich, 1952). In the winter of 1935 several hundred were sighted in the valley of the Tes-Khem River. They have been absent in the last decade in the Tuva district. In the Chuya steppe several hundred once lived permanently. In some years a considerable number penetrated from the adjoining regions of Mongolia, and their total population in the Chuya steppe reached several thousand (Bulavin, 1934; Kolosov, 1939). At present tens of Mongolian gazelle are found in Chuya steppe only in occasional years.

The total population of Mongolian gazelle throughout the range in the 1940's was about 1.5 million. Of these, about one million occurred in the Mongolian People's Republic where the population density was about 0.9 per km^2 of habitat. About 500,000 animals live in China.

Habitat. The most typical habitats of Mongolian gazelle are the plains or slightly hilly grass steppes and semideserts. They avoid highly irregular terrain and narrow valleys but may be encountered, especially in spring, along gentle mountain slopes. They enter shrubby thickets, sand dunes, or forests only in exceptional circumstances such as snowstorms (Lukashkin, 1927; Bannikov, 1951 and 1954). They inhabit altitudes of 100 to 1,900 m above sea level.

On the whole, two plant associations are most characteristic of Mongolian gazelle—feather grass semideserts and feather grass steppes. Less characteristic are grass-halophyte semidesert, and forb steppes, where Mongolian gazelle do not occur regularly, and mainly in winter. Mongolian gazelle rarely penetrate montane steppes with *tipchak* [oats] as ground cover and even more rarely halophytic or shrub deserts. They avoid cultivated fields. A typical
447 predominance of feather grass (*Stipa gobica, S. glareosa, S. orientalis*) with an admixture of sagebrush (*Artemisia frigida*) and saltwort (*Anabasis brevifolia, Nanophyton erinaceum*) represents the habitat for Mongolian gazelle in the Chuya steppe, Tuva district, and much of Mongolia. Other types of sagebrush, and also onions, often constitute much of the diet. In eastern Trans-Baikal adjacent regions of eastern Mongolia, and Barga (China), Mongolian gazelle are con-

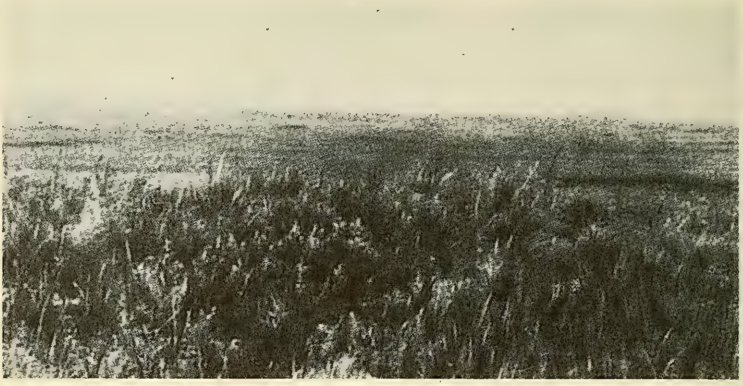


Fig. 143. Habitat of Mongolian gazelle in eastern Trans-Baikal. Photograph by A.N. Leont'ev.

fined mainly to those with feather grass in combination with snakeweed and *Agropyrum pseudoagropyrum* and more rarely, tansy steppes. These steppes are rich in forbs in the northern parts and in more humid places. Usually the plant cover of the habitat of Mongolian gazelle is extremely sparse; the estimated coverage is more often 5 to 20%, rarely reaching to 30 to 40%. The yield of herbage is low, from 0.5 to 0.7 to 3.0 to 5.0 c/ha.

Food. In the stomach contents of gazelle caught in Mongolia (22 samples; Bannikov, 1951 and 1954) remnants of 21 species of plants were found. However, the main food plants comprised four to six species. The important ones were feather grass (*Stipa capillata, S. gobica*) and multibulbed onion (*Allium polyrrhyzum*). Often Mongolian gazelle consume notable amounts of *Agropyrum pseudoagropyrum,* sagebrush, prostrate summer cypress (*Kochia prostrata*), and crested hair grass (*Koeleria gracilis*). Selective feeding on certain types of food by Mongolian gazelle is manifested in that they almost never touch snakeweed (*Diplachne*), which is abundant in the steppes. The stomachs of Mongolian gazelles caught in January contained 60% feather grass, and also shoots of derris, some unidentified grasses, and a little sagebrush. In spring the stomach contents included, apart from grasses and small amounts of sagebrush, flower buds of caragana, flower heads of snakeroot (*S. corzonera*), and seeds of unidentified legumes. The food of gestating and lactating females was more diversified than that of males.

Abundant green plants ensure in summer the moisture requirements of Mongolian gazelle. These animals are common in the plains at a distance of several dozen and even hundreds of kilometers from open water sources. In warm weather when there is such a source close to the pasture, they avidly visit it but can do without it (Bannikov, 1954). In Barga Mongolian gazelle often visit saline lakes in the early morning hours (Lukashkin, 1927).

In winter any water deficiency is readily compensated by snow. The suggestion (Radde, 1862; Yakovlev, 1926; Lukashkin, 1927) that Mongolian gazelle wander in winter in search of snow to quench their thirst is unfounded.

Home range. Mongolian gazelles are confined throughout the year to large or small herds which traverse considerable distances. In summer a herd grazes in an area of several hundred km^2, often moving from one place to another. In winter the herd is rarely
448 confined to a given site for more than a day or two. Even outside the period of migration, Mongolian gazelle traverse dozens of kilometers a day. The leaner the pasture and the larger the herd, the greater the daily wandering of the animals. In the period of migration they cover 200 to 300 or more kilometers per day. Only early in July, when the young are not strong enough, are females with young confined for a few days to the place of fawning; the fawning area of each female measures 2 to 3 km^3.

Daily activity and behavior. In winter, as well as in autumn Mongolian gazelle graze throughout the daylight period. In summer they leave their beds shortly before dawn, graze until 10:00 to 11:00 a.m. and later, after rest, again from 7:00 to 8:00 p.m. until twilight. At night gazelle evidently bed down. Their beds are situated somewhere on the leeward side of a small shrub; around them soft, warm, fine sand is blown. Sometimes in rocky sites gazelle dig up the soil slightly with their hooves. In winter they usually dig up the snow and lie in a small oval pit on the ground. Shelters are situated most often in hollows or on the leeward side of hillocks.

Mongolian gazelle are a hardy and fleet-footed antelope; they can run up to 60 to 65 km per hr and easily cover 12 to 15 km at such a speed. Their cardiac index is high—8.2 to 9.0 (Bannikov, 1954 and 1955). Gazelle run at a gallop, jumping vertically from time to time as much as 2 m off the ground. A normal jump is 4.0 to 6.0 m in length but, in the event of danger or hurtling an obstacle, a length of up to 13 m has been cleared (Lukashkin, 1927). When chased, gazelle invariably tend to cut back across the path of the pursuer. They avoid soft ground, sand, and sticky clay, and negotiate snow over 20 cm deep with difficulty. The weight load on the hoof is 700 to 1,100 g per cm^2. The animal slips on ice and cannot run fast on it. It is a good swimmer and, when required, can easily swim across such rivers as the Kerulen, Onon, and Argun (Bannikov, 1954).

Vision is extremely well developed in Mongolian gazelle; olfaction and hearing are rather poor.

Solitary Mongolian gazelle are exceptional; throughout the year they form large or small herds. In summer herds of 20 to 30 animals are more common; the largest herds at that time rarely reach 100. By the end of August or early September herds merge and the average herd strength is 60 to 80 animals. However, even at that time congregations of several hundred animals are not rare. In the period of rut, in December, herds remain large and are larger at the end of rut, in January to February. At that time, in favorable winters, herds in *Stipa* steppes consist on the average of 100 to 120 animals each. In this period, when snow occurs in forb steppes, herds run into several thousand or even tens of thousands. Large winter groups begin to break up only in May or June, i.e., after spring migrations. At the end of June, or slightly earlier, groups of gestating females separate, more often into groups of several dozen each; this, however, does not significantly alter the typical herd index for summer. In mid-July mixed herds of 20 to 30 animals with that year's fawns are seen. The sex ratio among adults from June to August (counts of 22 herds) is 1.0 male to 1.09 females (Bannikov, 1951 and 1954).

Seasonal migrations and transgressions. Mongolian gazelle usually exhibit distinct seasonal migrations every year. In normal years gazelle inhabiting mainly *Stipa* steppes in summer, sometimes with an admixture of saltwort and onions, or semideserts, gather by the end of August to September into large herds in feather grass-onion or feather grass-*Anabasis brevifolia*-onion steppes. With the exhaustion of *Anabasis brevifolia,* which disintegrates at its joints, and the withering of onions (mid-October), gazelle migrate into *Stipa* steppes located more to the north. These steppes serve well as pas-
449 tures right up to spring. There, in normal years Mongolian gazelle congregate at least during the first half of winter. Later, in January–February, in the event of snow, they move even more northward into forb steppes.

The assumption that freezing of steppe water sources in southern and central Mongolia, in the absence of snow, deprives gazelle of water and compels them to go northward for snow as a water substitute (Radde, 1862; Yakovlev, 1926; Lukashkin, 1927), is incorrect. On the contrary, northward migrations are associated not with the absence of snow in *Stipa* steppes but with its unusual abundance; in forb steppes in the northeast the snow cover is usually significantly less than in *Stipa* steppes lying more to the south. Moreover, uniform *Stipa* steppes, while satisfying the requirements of Mongolian gazelle early in winter, cannot feed them in January or later when large herds have gathered. In *Stipa* steppes at that time only feather grass stalks with sharp upper remnants remain. There is also significant snowfall by that time, which renders access to underground plant parts difficult. Migrations northward into forb steppes are distinctly seen in the eastern part of the geographic range of Mongolian gazelle, which even reach eastern Trans-Baikal. They partly congregate along the slopes of the Great Khingan or in the valleys of the Nonni and Sungari Rivers. In the western part of the range such migrations are less noticeable; gazelle reach there as far as the slopes of the Tannu-Ola range and into the valley of the Tes-Khem River. Another group of gazelles, mainly from the central part of the range, moves southward in midwinter into *Stipa* semideserts. They congregate along Gurban-Saikhan range, the uplands of the Gobi, Altai and the southern part of the Mongolian Altai (Bannikov, 1954).

The return spring migrations in normal years likewise occur gradually and subtly. From the region of *Stipa* desert steppes gazelle migrate usually into grass saltwort or *Stipa* steppes. They also move from northern forb steppes into *Stipa* steppes. These movements generally occur in mid-April.

In winters of less snow, especially those preceded by excessive summer precipitation, when the pasture is abundant, Mongolian gazelle may not undertake seasonal migrations. On the other hand, in years of abundant snow or in the event of ice-crust formation, migrations of gazelle are quite distinct. However, these migrations are disorderly and follow no definite pattern. Usually, large snowfalls or ice-crusted grounds, causing a lack in food availability, do not cover large expanses and occur only in the eastern or the western half of the geographic range. Over the last 50 years such phenomena have been recorded for the winters of 1911 to 1912, 1922 to 1923, 1925 to 1926, 1944 to 1945, and 1947 to 1948 in the eastern part of the range, and for the winters of 1926 to 1927 and 1935 to 1936 in the western part (Bannikov, 1954).

In the winter of 1944 to 1945 heavy snowfalls commenced even in November in the eastern half of Mongolia. The preceding summer had been extremely arid, which aggravated the situation. Hence Mongolian gazelle commenced southward migrations in November into *Stipa* desert steppes; large herds from Barga and Inner Mongolia also converged there at the same time. Unfortunately snowfall there in the first few days of December was even heavier than in the east. The gazelles dispersed. Reports of the appearance of large herds were received from extremely divergent regions. The herds could not remain in any one place and evidently suffered from hunger. At places traversed by them characteristic pits of 1.0 to 1.5 m diameter had been dug in the snow in search of food; under normal conditions gazelle do not behave in this manner. The drought of the preceding year rendered their search for food extremely difficult. The animals were compelled not only to dig up snow, but also to dig frozen soil for plant remnants concealed therein. Carcasses of emaciated animals were numerous. Early in December the animals moved north en masse. Moving farther and farther northward, they reached the Orkhon and Khara Rivers and the upper reaches of Kerulenin in central Mongolia. In Khentei they entered the forest where, in their search for food, they ate even shrubs; a large number died. Many gazelle gathered in mountain valleys and grazed on the mountain slopes.

450 Mongolian gazelle have recently started gathering in November in the northeast along the Ul'dzya River and in eastern Trans-Baikal. By December, on the left bank of the Ul'dzya River, several hundred thousands have been sighted. Snowstorms 150 km southward have not disturbed these wintering Mongolian gazelle and this part of the population has remained there until spring (Bannikov, 1951 and 1954).

The course of migrations of Mongolian gazelle in other years of *dzhut* followed a similar pattern. Thus, in the winter of 1911 to 1912 these gazelles went toward Hailar in northeastern China and found refuge from snowstorms in groves around the town. In that same year a gazelle was caught in the forest near the city of Irkutsk (Lukashkin, 1927).

A slightly different factor caused the migration of Mongolian gazelles to the western part of the geographic range in the winter of 1935 to 1936. Ice crusts in the basin of the Great Western lakes and in the Mongolian Altai caused the animals to wander in search of favorable places. They penetrated the northwestern part of Khangai and the slopes of the Tannu-Ola in the Tuva district, the valley of the Tes-Khem River, and in particular the northern slopes of the Mongolian Altai. They moved about for quite some time in extremely divergent directions, and a large number perished.

Hence, as a result of irregular but considerable amounts of snowfall within their range, regular directional migrations of Mongolian gazelle are weakly discernible.

In summer, however, Mongolian gazelle perform regular local migrations, which are determined by uneven and localized distribution of precipitation, as a result of which sections of semideserts or steppes almost totally devoid of grassy cover alternate with sections containing luxuriant herbage. In search of such extremely abundant pastures herds of gazelle regularly migrate, especially in the arid first half of summer. Summer migrations of gazelles from *Stipa* steppes into semideserts may also be caused by Brandt's voles [*Microtus brandti*], which intensely impoverish pasture when they occur in large numbers.

Reproduction. Rut in Mongolian gazelle commences at the end of November and terminates in early January, i.e., continues for slightly more than a month. Mating is preceded by a fairly prolonged courtship in which males chase females and utter loud guttural bellows. Skirmishes between males are common but not violent. Whether the gazelle is a polygamous or monogamous animal is not really known. "Harems" have not been reported; mating occurs in the herd.

Gazelles mate for the first time evidently at the age of 17 to 18 months. The exact period of gestation has not been established but, judging from the dates of mass mating and the birth of young, it probably lasts about six months.

Beginning in April female gazelles become extremely wary. Only males and a small number of barren females live in the plains at that time. Gestating females are confined to hilly sections of the steppe or to *melkosopochnika* [areas of small hills]. Scenting danger from afar, they attempt to avoid it long before its arrival by hiding some distance away. If the forewarning is short, they move off to the side and hide in hollows.

Fawning in the eastern and central sections of the range occurs in the first few days of July (Andrews, 1924; Bannikov, 1951). In the extreme western parts, in the Mongolian Altai and Chui steppe, it occurs at the end or middle of June (Sushkin, 1915; Kolosov, 1939). Births are generally simultaneously among females of a given population. At the time of fawning mothers usually remain in undulating steppes with deep hollows covered with derris shrubs or in *melkosopochnika,* i.e., in places where the young can hide easily on being separated for the first time from their mothers. Such sections where females gather for fawning occur throughout the range but more often in the southern half. Newborn fawns usually do not form large congregations and are found in groups of up to 20 to 30 animals. However, congregations of several thousand fawns have been reported, for example in 1919, in central Mongolia around Choyren (Andrews, 1924).

Over 90% of the females bear a single fawn; females with twins in July–August constitute 2.8%. The number of barren females among this gazelle is low; up to 68% have been seen with young in midsummer (Bannikov, 1954).

451 *Growth, development, and molt.* The first few days after birth the young remain lying anywhere in hollows, under shrubs, or

among tall derris. On sensing danger, they do not attempt to run away but press themselves to the ground, extend their neck forward, and lay their ears back. Young have been seen with adults after four, more often after six to eight days, of sighting the first newborn calves. The young begin to nibble grass around the tenth day. Lactation is still evident at the end of August (Bannikov, 1954) but information about its termination is not available.

Newborn fawns weigh 2.8 to 3.0 kg and are 51 to 56 cm long (two animals). At the age of one month they measure 74 to 82 cm (four animals) and at the end of September to early October are twice their length at birth. Horns on males are visible at the age of 3.5 to 4.0 months. By May of the following year they acquire adult stature (Bannikov, 1954). Longevity is not known.

Molt in Mongolian gazelle has not been thoroughly studied. Spring molt commences in the first few days of May and ends in early June. Autumn molt occurs, evidently, in October, since gazelle are still in summer wool by September but already sport a winter coat by November. The sequence of hair shedding is not known.

Enemies, diseases, parasites, mortality, competitors, and population dynamics. The wolf is the main enemy of Mongolian gazelle. Wolves take the maximum toll of gazelle at the end of winter, spring, and early summer. They are particularly successful in killing gazelle during snowy winters. In spring and early summer they lie in wait for gestating females going into *melkosopochnika* and hilly steppes. Packs of wolves are seen at places of fawning and they destroy calves in large numbers. Manul cats [*Felis manul*] and

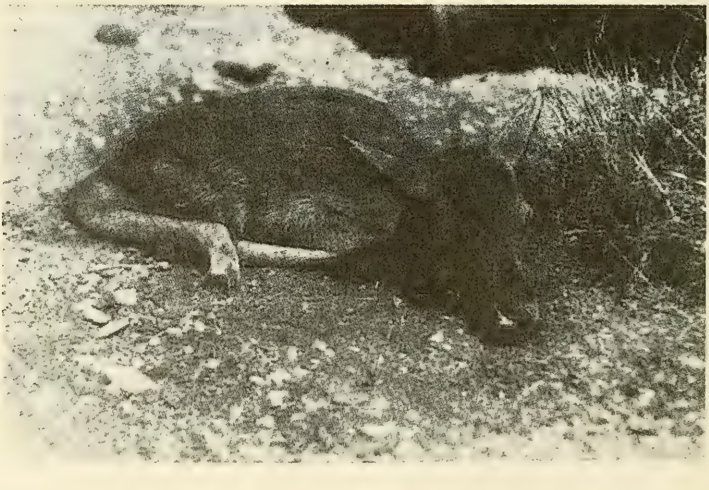


Fig. 144. A newborn Mongolian gazelle. June 8, 1951. Photograph by A.A. Yunatov.

golden eagle attack newborn fawns. Other predators, i.e., red fox, corsac fox, black kite, and buzzard [*Buteo*] consume only carcasses, as evident from wool and bones of Mongolian gazelle found in leftover food.

The diseases of Mongolian gazelle have not been studied. Some unverified information is available to show that they suffer from cattle plague. In captivity instances are known of necrobacillosis and hoof-and-mouth disease (Olikov and Nosova, 1940; Tsvetaeva, 1941). Mass mortality caused by an unidentified disease was reported in 1923 (Lukashkin, 1927).

The parasite fauna of Mongolian gazelle has not been thoroughly studied. Larvae of gadfly *Przevalskiana aenigmatica* and
452 nasopharyngeal gadfly *Pharyngomyia dzerenae* have been detected (Grunin, 1950). Parasitic flies of the family Hippoboscidae (*Melophagus* sp., Kolosov, 1939) have been seen in the wool, while mites are not uncommon in the ears. In Trans-Baikal *Echinococcus granulosus* has been found in the liver, heart, and lungs; tapeworm *Cysticercus tenuicollis* detected in the liver; and larvae of cattle tapeworm *Cysticercus bovis* recovered from the heart and skeletal muscles (Machul'skii, 1941). Nematodes have been found quite often in the intestines.

Sometimes Brandt's vole (*Microtus brandti*) is a serious competitor of Mongolian gazelle. In years of peak population voles overgraze pasture so much that the yield of vegetative mass drops more than tenfold. Furthermore, voles destroy primarily grasses, thereby greatly impoverishing pasture. The resultant food deficiency compels Mongolian gazelle to migrate from regions of high vole population, as occurred, for example, in 1929 and 1944 in Mongolia (Bannikov, 1954).

Among natural calamities, the most fatal for Mongolian gazelle are snowstorms, deep snow cover, and ice-crust. These phenomena cause not only migrations of gazelle, but also mass mortality, as observed in 1871 to 1872, 1911 to 1912, 1922 to 1923, 1925 to 1926, 1926 to 1927, 1935 to 1936, 1944 to 1945, and 1947 to 1948. In such winters gazelle perished directly from hunger or were killed by wolves. Weakened animals cannot negotiate snow swiftly. Moreover, during migrations gazelle often find themselves in unaccustomed conditions, for example in forests or narrow valleys, and thus become easy prey for predators.

The population dynamics of Mongolian gazelles are almost unstudied. As a result of death during ice-storms or deep snows, the population drops evidently two- or threefold and gazelle may disappear from some areas for a few years, as occurred, for example, in western Mongolia after the winter of 1935 to 1936. Barrenness is low; 60 to 70% of the females are seen with young in summer. About 80% of the fawns survive to autumn. Because of low fertility, however, population increase is slow and the annual increment is no more than 20 to 25% (Bannikov, 1951 and 1954).

Field characteristics. Mongolian gazelle are very easily distinguished by their much lighter color from goitered gazelle, both of which may be found together under similar conditions. Furthermore, unlike the sharp demarcation between the sandy-rust-colored flanks and the white underside of goitered gazelle, Mongolian gazelle exhibit a distinct gradual transition of sandy coloration of the flanks into the white underside, and their tail is light in color, not black, and much shorter. A running Mongolian gazelle holds its tail down and not up as in goitered gazelle. The build of Mongolian gazelle is much heavier and the neck shorter and thicker than that of goitered gazelle.

The track of a Mongolian gazelle is about 50 mm long and 30 to 40 mm wide; it is somewhat larger and broader than that of a goitered gazelle. Feces are in the form of black or dark brown pellets 9.5 to 16 mm long and 7 to 10 mm thick. Outside the period of rut Mongolian gazelle are silent. During rut the males emit a loud jerky bellow audible at some distance. At places inhabited by Mongolian gazelle circular beds are common, most often located on the leeward side behind small shrubs. (A.B.)

Economic Importance

In eastern Trans-Baikal hunting of Mongolian gazelle in the last century was most often done by chasing. When a large number of gazelle were found, the herd was driven onto ice where the helpless animals were killed with sticks, and up to 500 animals killed in a single chase (Cherkasov, 1867). At the end of the last century no more than 200 animals were caught annually in Trans-Baikal (Kirilov, 1902). In the Chui steppe hunting was likewise done by chasing; in the 1920's a hunter usually caught 6 to 10 gazelle each year (Bulavin, 1934). Hunting of Mongolian gazelle was banned in the USSR in 1933.

In Mongolia gazelle were long the prize targets of hunters. 453 Hunting was done by chasing and from concealment. In the latter a slow-moving camel was most often used as a cover. Automatic traps were set to catch gazelle, while hunting with a golden eagle was practiced in the western part of the country.[79] In the 1930's automobiles were used and 20,000 to 60,000 animals caught annually. In the 1940's the catch rose to 100,000 animals per year. The main hunting regions now are the steppes of eastern and central Mongolia (Bannikov, 1954).

---

[79] The reference to hunting with wolf hounds in Mongolia (Sokolov, 1959) is

The products obtained from Mongolian gazelle are excellent meat, hide and horns. The hide is used in making chamois or chrome leather; warm and light fur coats are stitched with the hairy winter hide but the hair falls out rapidly. Horns are used in making knife handles and other articles. The weight of a carcass with bones is 20 to 25 kg. The hide is 70 to 80 dm^2 in size.

The epizootic importance of Mongolian gazelle has not been studied. The possibility is not excluded that they transmit cattle plague and hoof-and-mouth disease. These gazelle are easily domesticated. They were formerly raised in semicaptivity in large parks and pens around Peking for purposes of hunting. (A.B.)

Subfamily of Goats

Subfamily Caprinae Gill, 1872

Species of moderate, and sometime large size, mostly stout, sometimes heavy in build with relatively short legs and a short neck; some are light and slender like gazelle. Back usually straight, but withers elevated in some; head set low.

Lateral hoof (of digits II and V) present. Middle hooves sometimes asymmetrical (*Ovibos*).

Facial part of skull moderately developed, sometimes slightly enlarged, or, on the contrary, small. Anteroparietal region wholly curved or bent in such a way that parietals are disposed on rear surface of skull. Skull pneumatization slight or absent, but sometimes significant. Preorbital depression on lacrimal distinct, slight, or absent. Ethmoid pit small or not developed. Nasals and premaxillae of normal development and sometimes adjoin each other; nostrils normal in size. Exceptionally, as a result of development of a proboscislike nose, premaxillae and especially nasals extremely shortened, anterior portion of maxillae elongated, and nostrils very large.

Cheek teeth usually hypsodont, with compressed crowns and sharply vertical ridges. Dental formula:

$$i\,\frac{0}{3},\ c\,\frac{0}{1},\ pm\,\frac{3}{3},\quad m\,\frac{3}{3} = 32;$$

in one case, $pm\frac{3}{2} = 30$, and in another $pm\frac{2}{2} = 28$.

erroneous. Wolfhounds (tazy) never lived in Mongolia in the past, nor do they live there now.

Incisors narrow and fairly uniform in width throughout their length; width gradually reduces from middle teeth to canines. Middle pair not distinctly broadened.

Horn size highly variable, ranging from tiny and no longer than the ears to large, massive, and heavy and considerably larger than the head in weight and volume. Horn shape also varies in different groups and species. The following main types are seen: thin short and conical, straight, or slightly arcuate; straight and bent in the form of a hook at the end; smooth or slightly rugose; thin horns of moderate length or long and slightly lyrate, or almost straight with annular tuberosity or tuberosities on anterior surface; large and thick, saber-shaped, heteronymously or homonymously bent, or intensely screwed in the form of a spiral, or rugose, or with tuberosi-
454 ties on anterior surface, or with flat or sharp (longitudinal ridge) anterior surface; massive horns bent sideways and down, later up and forward; large, massive, and heavy horns forming a gentle homonymous spiral turned sideways (sometimes "inverted"); and others.[80] Horns at the base have a circular cross section, are flattened from the sides, have a teardrop shape or are triangular, and sometimes with a rib on posterior surface. Horns usually black, light-colored in a few species, and semitransparent and wax-colored in one. Females usually sport horns, which are sometimes relatively large, differing little from those of males; usually, however, female horns are small. Females of some species without horns, while in other species only a few females bear horns.

Tip of muzzle normal in size, densely covered with hair, or with a more or less bare batch at the end between the nostrils, usually with a vertical, sometimes bare furrow on upper lip, extending from edge of lip to nose bridge, often along it. Exceptionally, snout highly swollen and extends into a well-developed proboscis-like formation, with nostrils turned down, or only slightly enlarged and swollen sideways with nostrils set forward.

Skin glands well developed and seen in different forms in different numbers, varying degrees of development, and combinations. Apart from hoof, carpal (knee), preorbital, and inguinal glands, glands behind horns and caudal glands may also be present. Sometimes the animals, especially males, are characterized by a particularly pungent smell (goaty). Tail well developed, but short, sometimes with a tassel at the end, rarely rudimentary, and sometimes triangular in cross section with a flat undersurface and bare below. Dewlap absent.

---

[80] For an explanation of some of the terms used, see the description of sheep (*Ovis*).

Pelage highly variable. In some species short, close-fitting, and fairly uniform in length throughout the body; in other species relatively uniform but long and shaggy. Moreover (partly as a seasonal variation in winter coat or as a sex characteristic), beard may be present on chin, a long tress on throat, neck, chest, and upper portion of anterior legs, or a mane on the upper part of neck, shoulders, and withers.

Color usually fairly uniform or with darkening or lightening in some sections, yellow and brown shades, sometimes brown or dark brown, and black or pure white exceptionally. Transverse streaks not seen and facial pattern usually not developed. Sometimes a fairly contrasting dark- and light-colored pattern occurs on the legs. Sexual dimorphism in coloration not evident but there are differences in horn growth (see above) and ornamental hair (mane, etc.). As a result of living under severe climatic conditions, usually a fairly perceptible, sometimes very marked (more than in other subfamilies) seasonal dimorphism exhibited. Teats two or four.

The subfamily is presented here in a wider perspective than generally acknowledged (according to Simpson, 1945; also Sokolov, 1953), and includes groups which older investigators (even some contemporary ones) usually regarded as distinct subfamilies—Saiginae, Pantholopinae, Rupicaprinae, Caprinae, and Ovibovinae. It includes species which are extremely divergent in their overall appearance. The subfamily includes the gazelle-like "antelope", saiga and orongo (chiru), goats and sheep, and forms intermediate or close to them (tahr, nahur or kuku-yaman [blue sheep], and Barbary sheep), chamois and the chamois-like goral and forms close to them, and finally the large cow-like musk ox and takin. Caprinae represent the most variegated and heterotypical subfamily of Bovinae.

This subfamily is a highly eurybiotic group, the species of which survive from extreme Arctic latitudes to torrid desert mountains of the tropics, and from sea level to extremely high altitudes. They are inhabitants of diverse, usually very high mountain regions, often the highest altitudes, montane forests or rugged and rocky regions, and even regions at sea level and very low altitudes. Exceptionally 455 they inhabit high Arctic tundras, steppes, semideserts and high plateaus (Tibet). They live in groups or small herds but are sometimes solitary. One species forms large herds.

The range of the subfamily (reconstructed) is very extensive and encompasses the Old and New World. In Africa it covers the northern part of the mainland in the south as far as Rio de Oro and the southern part of Mauritania,[81] Adrar-des-Iforas, tributaries of the Niger River, Air (Azbine), Tibesti, Ennedi, Kordofan, and Ethiopia. In Eurasia species of the subfamily are distributed in the Iberian Peninsula and the Pyrenees, Alps, and Apennines, in Sardinia and Corsica, the Balkans, islands of the Grecian archipelago, and the Carpathians. From the foot of the Carpathians along the steppes of the European and Asiatic parts of the USSR, the range of this subfamily extends to and includes the Altai, Sayans, Trans-Baikal mountains, northern Mongolia, mountains of the Far East and northeastern Siberia, and also part of northern Siberia from the right bank of the lower reaches of the Yenisey to the Chukchi Peninsula, at places to the Arctic and Pacific Ocean coasts, and Kamchatka.

To the south of this region Caprinae are found in the Amur and Ussuri regions, some parts of Mongolia, Dzhungaria, Kashgaria, northern Kuril Islands, Honshu, Shikoku, Kyushu, Taiwan, Tibet, the Himalayas; Malacca and Sumatra, India, Afghanistan, Iran, Middle Asia, the Caucasus, Asia Minor, Syrian region of the United Arab Republic, Palestine, and the Arabian Peninsula.

In North America the range of the subfamily covers Alaska in the east almost up to the Mackenzie (in the eighteenth century probably also a part of the Aleutian chain), the western half of the mainland, in the south to central Mexico (Chihuahua), and in the east to Texas, Nebraska, and the Dakotas, i.e., roughly up to 100° on the east. Along the tundras in the northern part of the mainland, the range runs in the east almost to Hudson Bay, covers the Arctic archipelago (except Baffin Island and Melville Peninsula), and the northwestern and northern half of the east coast (in the south to 70° N lat.) of Greenland.

The animals are extinct at present over fairly large expanses. Some species are acclimatized beyond the limits of the range shown above (mouflon in central, western, and eastern Europe; chamois, tahr, and blue sheep in New Zealand). In a purely geographic context the group could be considered Old World, predominantly Eurasian. It is dispersed throughout the world in a domesticated state.

The subfamily includes several extremely characteristic forms and groups which exhibit no distinct direct phyletic affinities with representatives of other subfamilies. In this context the majority of species of this subfamily appear rather sharply isolated. Within the family, the Caprinae occupy a somewhat peripheral position as a fairly specialized group. Phyletic affinities are more definitive between Caprinae and Antilopinae and within the latter to Antilopini. These affinities are apparent in the genera *Saiga* and *Pantholops* (Saigini). The purely peripheral position of these genera is reflected in their recognition as an independent (or two independent) intermediate group in some classifications, or even their assignment to Antilopinae.

---

[81] Information about Rio de Oro and Mauritania dubious.

Members of the subfamily are known from the Lower Pliocene and even the Upper Miocene of Europe and Asia as fairly specialized forms. In America and Africa species of the subfamily have been detected only from the Pliocene. Thus, in origin this group should be considered Eurasian and only recent inhabitants of Africa and America. All fossil forms belong to Recent groups (tribes); furthermore, only one (Saigini) is known from the Pliocene, while all the others have been found even in much earlier formations, i.e., they arose a long time ago. The division of the group into major branches occurred evidently in the Middle or even the Lower Miocene (Sokolov, 1953). Recent genera are not found beyond the Pliocene and only one (*Ovis*) is known from the Upper Pliocene.

457 The subfamily consists of some distinct natural groups to which recent specialists in the field of systematics and authors of monographs usually assign tribes. Each consists of a small number of species. Considerable unanimity over genera of Caprinae exists although apparently it is possible to reduce their number further (*Capricornis, Ammotragus,* and *Pseudois*). The number of species in the group is fairly well known and differences occur only over species of true goats, i.e., genus *Capra.*

The subfamily is divided into four tribes: Saigini (chiru, *Pantholops;* saiga, *Saiga*); Rupicaprini (goral, *Nemorhaedus;* serow, *Capricornis;* snow [Rocky Mountain] goat, *Oreamnos;* chamois, *Rupicapra*); Ovibovini (takin, *Budorcas;* musk ox, *Ovibos*); and Caprini (tahr, *Hemitragus;* goat, *Capra;* blue sheep, *Pseudois*; Barbary sheep, *Ammotragus;* sheep, *Ovis*).[82]

The subfamily comprises 30 genera of which 17 are extinct (9 of Ovibovini) and 13 extant (about 24% of present-day genera of the family). The total number of species is 22; one species each in genera of chiru, *Pantholops* (*P. hodgsoni*); saiga, *Saiga* (*S. tatarica*); and goral, *Nemorhaedus* (*N. goral*); two species in genus serow, *Capricornis* (*C. sumatraensis* and *C. crispus*); one species each in genera Rocky mountain goat, *Oreamnos* (*O. americanus*); chamois, *Rupicapra* (*R. rupicapra*); takin, *Budorcas* (*B. taxicolor*); musk ox, *Ovi-*

---

[82] Another combination has also been suggested: Pantholopini, Saigini, Nemorhaedini (Rupicaprini excluding *Oreamnos* and *Rupicapra*), Ovibovini, and Caprini (including *Oreamnos* and *Rupicapra*) (Sokolov, 1949 and 1953).

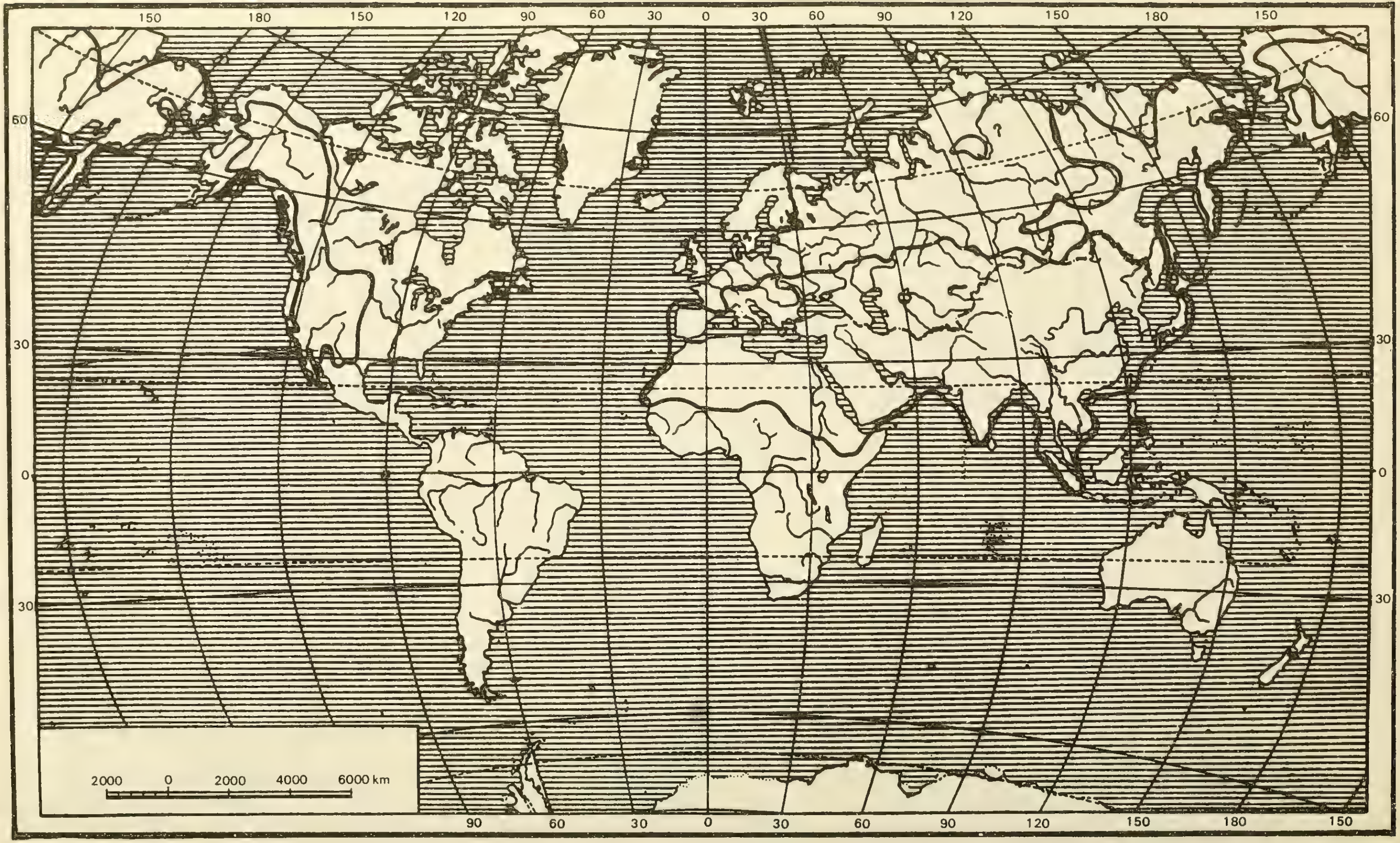

150
180
150
120
90
60
30
0
30
60
90
120
150
180
150
60
30
0
30
?
2000
0
2000
4000
6000 km
90
60
30
0
30
60
90
120
150
180
150

Fig. 145. Reconstructed geographic range of subfamily of goats, Caprinae. Question mark in central Siberia denotes region of probable, but not established, habitation of members of the group (snow sheep) between the Lena and Khatanga. V.G. Heptner.

bos (*O. moschatus*); and tahr, *Hemitragus* (*H. jemlahicus*); eight species of mountain goat, *Capra* (see description of genus); one species each of blue sheep, *Pseudois* (*P. nayaur*) and Barbary sheep, *Ammotragus* (*A. lervia*); and two species of sheep proper, *Ovis* (*O. ammon* and *O. canadensis*). Thus, about 21% of the species belong to Caprinae.

Of the 13 genera two are American (*Oreamnos and Ovibos*),[83] one African (*Ammotragus*), one Eurasian-American (*Ovis*), one Eurasian-African (*Capra*), two Eurasian (*Saiga* and *Rupicapra*), and the remaining six Asian. Of the species, one is African, one or two European, one Asian-African (or Eurasian-African), one American-Asian, three Eurasian, and eleven or twelve Asian. Thus, not only in origin and distribution, but also in distribution of genera and species, the subfamily represents a distinct Eurasian, predominantly Asian, group.

These are game and table animals. Two species, goat and sheep, survive in a domesticated state and constitute extremely important farm animals.

In the USSR there are five genera (about 38% of present-day genera), namely, *Saiga, Nemorhaedus, Rupicapra, Capra,* and *Ovis,* and nine species (about 41% of present-day species) constituting about 3% of species of Russian fauna.

These genera are inhabitants of steppe and montane regions in the USSR. They are objects of sport and hunting. Hunting of some species is partly or totally prohibited. (V.H.)

Genus of Saiga

Genus *Saiga* Gray, 1843

1843. *Saiga.* Gray *List. Mamm. Brit. Mus.,* p. 26. *Capra tatarica* Linnaeus.

1844. *Colus.* Wagner. Schreber's *Säugethiere. Supplem.,* vol. 4, p. 419. *Antilope saiga* Pallas. (V.H.)

Animals of moderate size and fairly light build, similar to gazelles.

Facial part of skull sharply altered and reduced. Nasals very short. General skull size about half that of other genera and width about one-half of length. Suture between nasals and between nasal, 458 frontal, and partly lacrimal completely obliterated early in life.

---

[83] In the Quaternary period *Ovibos* was widely distributed in Eurasia and were Old World in origin.

Nasals set straight forward and slightly upward. Premaxillae very small, broadened like a spatula in front, and anterior portion of maxillae intensely elongated; premaxillae and maxillae do not come into contact with nasals. Lacrimals very large and project forward with their anterior part strongly broadened in dorsoventral direction. Nasal orifices fairly large and open high up, not only forward but upward. They are bounded on the sides by lacrimals to a significant degree (only case in the order). Anteroparietal region of skull rather gently flexed. Skull poorly pneumatized. Preorbital depression on lacrimal very faint. Ethmoid pit absent. Orbits tubular. Dental formula:

$$i\,\frac{0}{3},\ c\,\frac{0}{1},\ pm\,\frac{3}{2},\ m\,\frac{3}{3} = 30;$$

in fossil (S. *prisca*?) evidently pm $\frac{3}{3}$ = 32.

Horns of moderate dimensions, thin, set almost vertically, with an insignificant lyrate bend and sharply projecting annular ridges throughout (except upper part). Keratin semitransparent and light waxy in color. Females without horns.

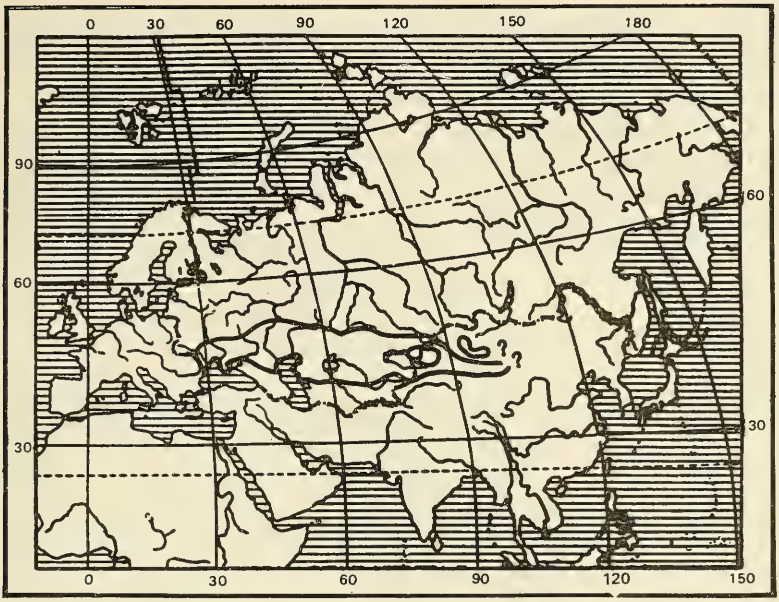
Snout highly swollen and projects in the form of a small proboscis which hangs down slightly. Nostrils small, circular, set downward, with no bare patch at the end of the snout. Preorbital glands and their openings small; carpal glands, hoof glands on front and hind legs, and two very small inguinal glands (located in special folds very close to the teats) present. No specific pungent smell. Tail very short and without tassel at the end.

Pelage of uniform length, but in winter with something like a short mane on neck. Beard absent. Sharp seasonal dimorphism seen in density and length of fur and its color. Sexual dimorphism mani-
459 fested only in slightly smaller size of females and absence of horns. Teats four (front pair very small).

Steppe and semidesert forms living in large herds.

Geographic range (reconstructed) covers the steppes of the USSR from the eastern foot of the Carpathians to the Altai foothills, Dzhungaria, and the western Mongolian Republic.

Genus *Saiga* is closer to genus *Pantholops* (chiru, Tibet) with which it is often combined into a common group (subfamily or tribe). Yet differences between these genera are extremely marked and genus *Saiga* stands generally well isolated. As mentioned above, genus *Saiga* (and genus *Pantholops*) may be considered a form linking to some extent Caprinae with Antilopinae and some researchers even place it in the latter. Simultaneously, however, in the structure



458 Fig. 146. Reconstructed geographic range of genus *Saiga* Gray, and species range of *Saiga tatarica* L. A.G. Bannikov.

of the hoof glands, for example, genus *Saiga* exhibits features of similarity with genus *Ovis* (sheep).

The origin of the genus is vague and paleontologically this question cannot be resolved just now. Fossil remains are known only from the Pleistocene and belong to fairly typical forms, like Recent saiga. At the same time the high morphological specialization and geographic and ecological features of the genus sharply isolate it from other members of the subfamily and compel us to place its origin in the far distant past, at least in the Upper Pliocene.

Saiga were widely distributed in the Pleistocene; in the west they inhabited central and western Europe and reached England; in the east they penetrated northeastern Siberia as far as the Yana estuary and New Siberian Islands and, according to recent data, thrived even in Alaska.

Apart from common saiga, saiga of northwestern Mongolia were described as a distinct species under the name *S. mongolica* Bann. The differences between the two forms are fairly marked, but nevertheless it would be more correct to regard Mongolian saiga as only a subspecies of common saiga. Thus the genus consists of only one species, *Saiga tatarica* Linnaeus, 1766, representing about 4.5% of species of the subfamily.

There is one species in the USSR, constituting 0.3% of species of Russian fauna. This species is an inhabitant of steppes and semideserts.

S. tatarica is a game animal, hunted for its meat, hide, and horns; the latter are used in Tibetan medicine. As a result of the cultivation and colonization of steppes and direct persecution, the range of the animal has shrunk considerably. (V.H.)

13. SAIGAK, SAIGA

***Saiga tatarica* Linnaeus, 1766**

1760. *Ibex imberbis.* Gmelin. *Nov. Commentarii Acad. Scient. Petropolitanae,* vol. 5, p. 345. Tara on Irtysh. Name pertains to saiga but given in a work where binomial nomenclature has not been used. It is of no importance in nomenclature.

1766. *Capra tatarica.* Linnaeus. *Systema Naturae,* 12th ed. Steppes along the Ural [River].

1766. *Antilope saiga.* Pallas. *Miscell. Zool.,* p. 6. Substitute for *Ibex imberbis.*

1767. *Antilope scythica.* Pallas. *Spicil. Zool.,* vol. 1, p. 9. Substitute for *Ibex imberbis* Gm.

1768. *Capra sayga.* Forster. *Philos. Trans.,* vol. 57, p. 344. Volga region.

1816. *Cemas colus.* Oken. *Lehrb. d. Naturgasch.,* vol. 3, pt. 2, p. 736. Substitute for *Ibex imberbis.* (V.H.)

Diagnosis

Genus *Saiga* consists of just one species.

Description

S. tatarica resembles a small sheep standing on long thin legs but is much lighter in build. Withers slightly higher than, or equal to, height of sacrum. Head large. Intensely swollen and puffed snout overhangs mouth and forms something like a short and soft mobile
460 proboscis. Nostrils circular, set very close to each other, and turned down. Bare skin patch at end of snout absent. Ears short, with rounded tips, and covered with wool inside and out; length and width of ears almost equal. Eyes large and dark brown; pupil elongated-oval. Tail short, with slightly elongated hair at end. Hooves large and broad; forehooves 55 to 68 mm long and 42 to 54

mm wide. Hind hooves about 10% smaller than forehooves. Accessary (lateral) hooves small, about 10 to 14 mm long.

Horns semitransparent and a light waxy color; only extreme tips dark-colored. Horns set almost vertically, slightly turned back, with a faint lyrate flexure. Along much of their length (except for upper one-third) carry up to 18 to 20 (more often 12 to 14) annular ridges; last 3 or 4 distal ridges do not form a full circle and are distinctly seen only on front surface of horn. Females without horns.

Hair distinctly separated into guard hair and fluffy underfur.[84] Former straight and long, while latter thin and curly and only one-half length of guard hair. In different areas of body, 1.0 cm^2 area of skin contains 15 to 101 guide hairs, 47 to 200 guard hairs,* and 1,100 to 2633 follicles of underfur. Amount of hair per unit area almost the same in summer and winter; ratio of number of different types of hair also undergoes little change. However, winter hair 50 to 70% thicker than summer hair. Underfur becomes particularly thickened in basal one-third part in winter (Adol'f, 1959).

Length of fur and color of animals subject to seasonal changes. In summer hair throughout body fairly uniform in length (18 to 30 mm). In winter wool twice as long (40 to 70 mm). Moreover, hair on sacral patch greatly elongated (see below); hair on neck of males highly elongated and forms almost a mane, 120 to 150 mm long. Equally long hair also grows on snout under the eyes ("side whiskers").

General color shade of summer coat yellowish-rusty. Flanks somewhat lighter in color than back. Abdomen and chest white, distinctly set off from sandy-rusty flanks. No light-colored speculum on rear of thighs. Upper portion of neck darker than sides. From
461 occiput, along top of neck, a broad streak of slightly more intense coloration than general color of back is visible; in shoulder region, especially sacrum, even darker-colored fields form. In old males darkening particularly well manifested and brownish patches seen on sacrum and shoulders. Legs sandy-yellow but darker in front. On joints, especially of forelegs, brownish spots distinctly seen.

Upper part of head of adult males dirty white, roughly up to line joining midpoints of eyes. Forehead and crown dark rusty with an admixture of white, as a result of which some color variegation seen. Light sandy-colored ring occurs around eyes and a diffuse white

---

[84] Adol'f (1959) distinguishes another type—guide hair—among the guard hair.* Sokolov's statement (1959) that no distinct separation of hair into guard hair and underfur occurs is erroneous.

*It is not clear what distinction is made between guard and "guide" hairs—Sci. Ed.

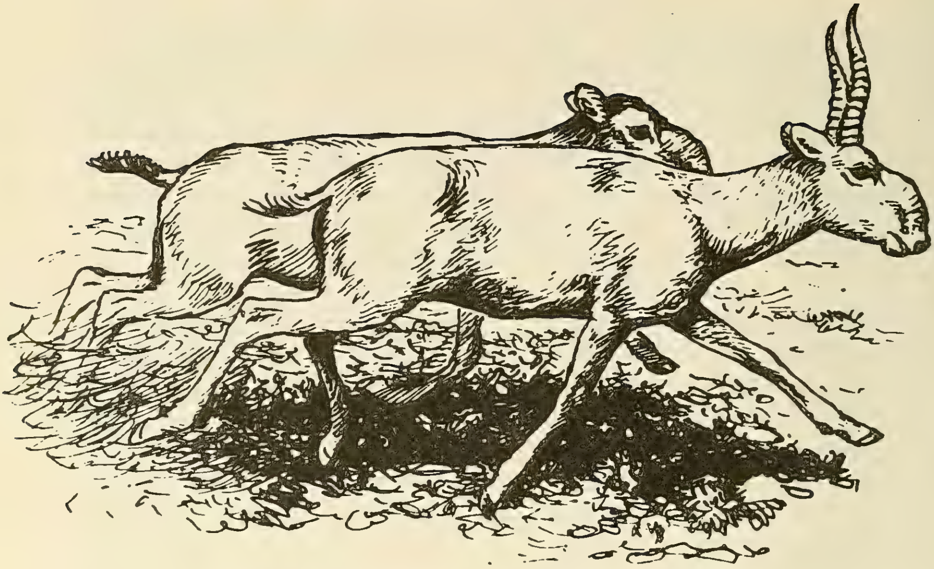


Fig. 147. *Saiga tatarica* L. Sketch by A.N. Komarov.

patch under them. Cheeks yellowish-rusty and same shade as sides of body. Distinct border of brown hair occurs along outer edge of ears. Tufts of long, black vibrissae seen on lips and around nostrils. Upper portion of tail covered with brownish-yellow hair, which becomes slightly longer toward end of tail. Color variegation of forehead and crown weak in females and upper portion of nose sandy-yellow. In young, forehead, crown, and nose rusty-yellow.

General color of winter coat very light, dull, and clayey-gray. Throat, chest, and abdomen whitish with brownish-gray tinge. Much darker color on back turns lighter on flanks and merges gradually into much lighter color on abdomen. In sacral region a dark brownish-cinnamon, sometimes almost black, patch roughly 7 cm × 4 cm occurs, consisting of long dark hair twice the length of light-colored hair elsewhere on back; similar grayish-black spots occur on cheeks, under the eyes. Cheeks, except for these spots, and sides of neck gray with a brownish tinge; these two gray streaks perceptibly darker than color of flanks and back, and particularly dark in old males. Albinism occurs now and then but melanism very rare.

Measurements[85]: body length of adult males (n = 31) 123 to 146 cm (M 132) and females (n = 25) 108 to 125 cm (M 116); height of

---

[85] Measurements and weights given are those of mature saiga of the nominal form caught on the right bank of the Volga.

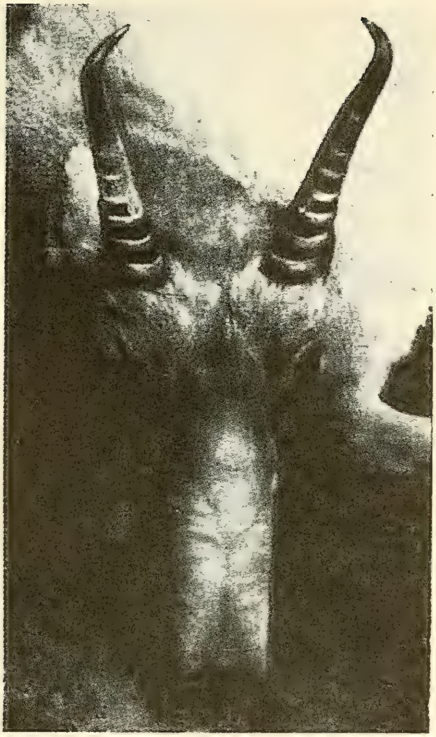


Fig. 148. Head of year-old male saiga in summer coat. Photograph by A.G. Bannikov.

males at withers 69 to 79 cm (M 73) and females 57 to 73 cm (M 68); height of males at sacrum 60 to 73 cm (M 65.5) and females 57 to 69 cm (M 62.5); diagonal* length of torso in males 76 to 92 cm (M 84) and females 61 to 88 cm (M 77); tail length of males without terminal hair 8.0 to 12.5 cm (M 10) and females 6 to 10 cm (M 8.5); length of ears in males 8 to 12 cm (M 11) and females 7 to 11 cm (M 8.5); and horn length along curvature 28 to 38 cm (M 32.5). Weight[86] of males (n =29) 32.5 to 51 kg (M 43.1) and females (n=25) 21.4 to 40.9 kg (M 30.8). Condylobasal length of skull in males (n = 30) 222.3 to 250 mm (M 240.2) and females (n = 30) 205.4 to 228.6 mm (M 217.8) (A.G. Bannikov).

Skull characteristics given in description of genus.

[86] Weight, especially in males, varies sharply in different seasons (see below). For Kazakhstan the average weight of males is 45.7 kg and of females 36 kg (Sludskii, 1955).

*Apparently from point of shoulder to point of pelvis—Sci. Ed.

Taxonomy

See description of genus.

Geographic Distribution

S. tatarica are found in the steppes and semideserts of Eurasia from the eastern foot of the Carpathians to the foothills of the Altai, western Dzhungaria, and basins of the Great Western lakes in Mongolia.

Geographic Range in the Soviet Union (Reconstructed)

The western extremity of saiga distribution in the seventeenth and eighteenth centuries was represented by the Carpathian foothills and evidently Southern Bugge and Prut Rivers, i.e., roughly 25° E long.[87]; the northwestern corner of the range lay at the intersection of 25° E long. and 50° N lat. (Rachinskii, 1745*; Güldenstädt, 1787*; Gerbershtein. 1808*; Meyer, 1794*; Greve, 1898[88]; Brauner, 1923; and others). Saiga disappeared from Moldavia in the early eighteenth century (Harper, 1945). The northern boundary in Europe ran slightly south of Kiev and along the line of Kursk, Usman, Tambov, Samara[89] (Kuibyshev), and Ufa. Near Ufa in some years saiga reached north to 55° N lat. (Pallas, 1777*; Beber, 1792*; Litvin, 1889*; Levchenko, 1892 [1882 ?]; Zyablovskii, 1806; Kir'yakov, 1837; Köppen, 1891*; Pliginskii, 1929). According to Rachinskii (1745) early in the eighteenth century saiga were encountered close to Uman, Novaya Secha, and in the basins of Tashlyk, Sinyukha, Mertvye Vody, Ingul, Ingulets, Kozhnaya, Akchachakhrak, and Karachakhrak Rivers. In the south in the seventeenth and eighteenth centuries, saiga were distributed as far as the Black and Azov Seas, but were already absent in Crimea from where only several paleolithic finds are known (Gromov, 1948). More recent finds have been unearthed at the boundary between Azilian and Tardenoisian cultures (Gromov, 1937), along with much earlier finds from the second

---

[87] References to saiga inhabiting central Poland (Kyuv'e, 1817; Desmare, 1822; Byuffon, 1764) do not contradict this delineation because they pertain to the Polish borders of 1768.

[88] Greve has given a more complete review of the distribution of saiga in the historic past. In all the latest works on the range dynamics of saiga for the seventeenth to the nineteenth centuries, his data has been incorporated.

[89] Saiga are depicted in the coat of arms of the city of Samara.

*Not in Literature Cited—Sci. Ed.

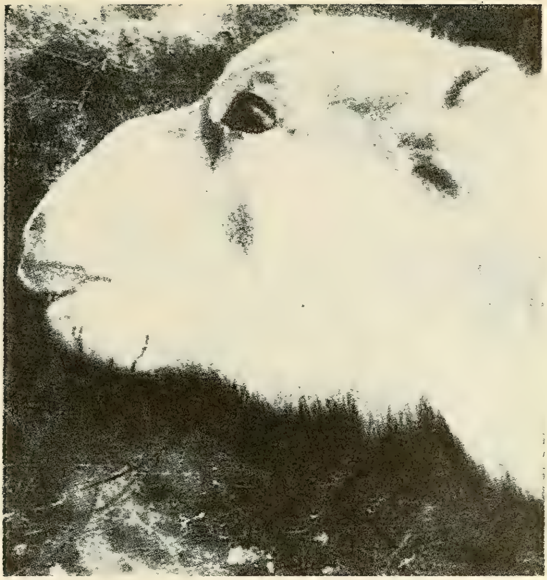


Fig. 149. Head of female saiga in winter coat. Photograph by A.G. Bannikov.

century B.C. to the second century A.D. (Tsalkin, 1954).[90]

In the western Cis-Caucasus saiga reached in the south to the 463 Kuban.[91] In the eastern Cis-Caucasus saiga undoubtedly reached the Caucasian foothills and the southern boundary of the distribution of the species intersected the lower reaches of the Terek. How far south saiga penetrated along the coast of the Caspian Sea remains vague; presumably the boundary of their range descended roughly to Derbent. Even farther south, from Apsheron, only Upper Pliocene finds are known (Bogachev, 1939); saiga from the Riss-Wurm period have been described from Binagadov close to Baku (Alekperova, 1955). Thus saiga lived throughout the European steppe and much of the forest-steppe zones. However, saiga penetrated the forest-steppe only in summer and not every year.

Saiga disappeared at the end of the eighteenth century from those northwestern parts of their range colonized earliest by man. At that time the animals seldom crossed to the right bank of the Dnieper and extended north to the line Dnepropetrovsk–Volsk–Samara River–Obshchii Syrt (Bronevskii, 1834*; Chernoi, 1853; Novitskii, 1907*; Levchenko, 1892 [1882?]; Sidorov, 1928*; and others). At the end of the eighteenth century in the Volga-Ural steppes and farther east the range evidently had still not shrunk. Saiga appeared on the Samara River, penetrated deep inside Bashkiria during years of drought, inhabited Mugodzhara, and extended as far as Orenburg, Orsk, and Kustanai (Pallas, 1778; Lepekhin, 1821; Rychkov, 1762; Borodin, 1891; Zarudnyi, 1897). Farther eastward saiga were encountered in the north to Ishim, Kulunda and, crossing the Irtysh, penetrated to the Ob', i.e., in the summer reached the Barabinsk steppe (Rychkov, 1762; Gmelin, 1771; Pallas, 1773). Farther away, along the foothills of the Altai and through the Zaisan depression, the northern boundary of distribution of saiga extended into China. The southern boundary of their range in Asia proceeded from Kara-Bogaz-Gol in the lower reaches of the Amu-Darya, middle reaches of Syr-Darya (roughly at the intersection of the latter with 44° N lat.), and farther, along the foothills of the Karatau, Kirgizia and the Trans-Ili Alatau, and along Ili River valley into China. Saiga naturally were absent in the Dzhungarsk Alatau and Tarbagatai, but 464 inhabited the Alakul' depression (Potanin, 1856; Grigorev, 1861; Pettsol'd, 1877).

---

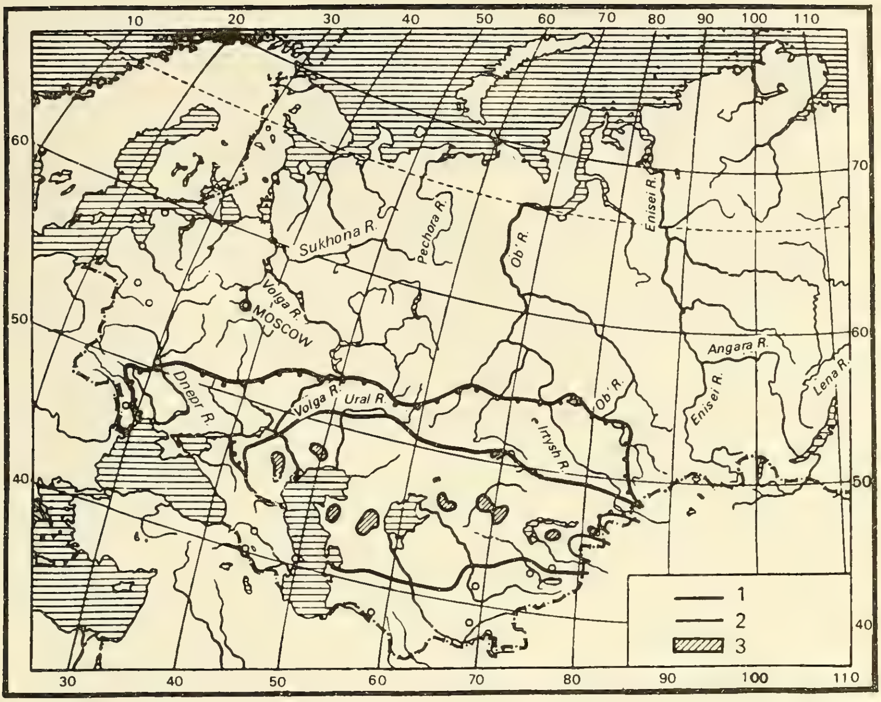
[90] Puzanov (1949) believed that saiga became extinct in Crimea after the arrival of the Tatars.

[91] On the Kuban saiga have also been found at the Ilsk site (Mousterian period; Gromov, 1948) but not farther south because of the terrain. In the map given by Adol'f (1957) saiga are shown for the eighteenth century as far as Sochi and the western parts of the main Caucasian range, which no doubt is an error. The animal could hardly have lived as far north and northwest of Kiev as shown in Gromov's map since broad-leaved forests occurred there.

The sharp reduction of the range of saiga in Europe continued in the nineteenth century. By the middle of that century they no longer crossed to the west bank of the Don and only a few individual animals were reported on occasion there. The northern boundary traversed close to Tsaritsyn (Stalingrad) [Volgograd] but, time and again, transgressions to the north as far as Kamyshinsk and Ural'sk were reported. Intense *dzhut* in the Volga-Ural interfluve region in 1826–27 led to the disappearance of saiga from this region for a few decades. Later, in the east the northern boundary of the range of saiga proceeded through Temir, Turgai, the Chingiztau range, and Bayan-Aul to the northern shore of Lake Zaisan (Glich, 1879; Levchenko, 1892; Sidorov, 1928; Zheleznov, 1857; Severtsov, 1861; Bazhanov, 1929; Satunin, 1896; Karelin, 1861; Tolstoi, 1906; Borodin, 1891; Zarudnyi, 1897; Silant'ev, 1898; Sludskii, 1955). In the south saiga were still common in the early nineteenth century in the Sal'sk steppes and reached Stavropol, but were a rarity on the Kuma River (M. Zhitkov, 1849; Zyablovskii, 1806; Vanyukov, 1868; Dinnik, 1910; Beme, 1936). The southern boundary in the Asian part of their range

---

*Not in Literature Cited—Sci. Ed.


10
20
30
40
50
60
70
80
90
100
110
60
50
40
70
60
50
40
30
40
50
60
70
80
90
100
110
Sukhona R.
Pechora R.
Ob' R.
Enisei R.
Volga R.
MOSCOW
Angara R.
Dnepr R.
Volga R.
Ural R.
Ob' R.
Irtysh R.
Enisei R.
Lena R.
1
2
3

463 Fig. 150. Distribution of saiga, *Saiga tatarica* L.

1—first half of eighteenth century; 2—range in 1957 and 1958; 3—range in 1920's and 1930's. A.G. Bannikov.

evidently did not change much at that time.

From the end of the nineteenth to the early twentieth century a further sharp reduction in range took place, which continued right up to the end of the 1920's and early 1930's. By then, in the European part of the USSR saiga survived only in the uninhabited regions of the Kalmyk steppe and evidently disappeared altogether from the Sal'sk and Karanogaisk steppes (Sytin, 1927; Berkov, 1927; Baranov, 1927; Orlov, 1928; Heptner and Formozov, 1941). In the Volga-Ural steppes saiga remained only near the Kamysh-Samar lakes; farther away they were met with in the Buzachi Peninsula, the Ustyurt, east of the Emba River, in the Pri-Aral Karakums, Sary Su valley, in the western part of Bet-Pak-Dala, in southern Pribalkhash, i.e., the Ili-Karatal interfluve, along the Bakanas, and at the southern extremity of Lake Alakul'. Saiga were never reported in the eastern half of Bet-Pak-Dala, in northern Pribalkhash, and the Zaisan depression. The range of saiga was highly fragmented (Kashkarov, 1932; Sludskii, 1955; Rakov, 1956; Kuznetsov, 1928; and others).

Commencing from the end of the 1920's in the European part of the USSR and from the 1930's in Kazakhstan, the range of saiga was restored. By the 1940's they had already reached 48° N lat. on the right bank of the Volga, in the west to Ergenei (roughly 44° E long.), in the southwest to Manych, and in the south to the Kuma River (Babenyshev, 1948; Adol'f, 1950; Bakeev and Formozov, 1955). At about this same time saiga were again sighted in the Volga-Ural steppes and their area of distribution enlarged in the Ural-Emba steppes, Ustyurt, and Bet-Pak-Dala (Kolosov, 1935; Kuznetsov, 1948; Stroganova, 1952; Rakov, 1956).

Drought in the years 1945 to 1951 and very snowy winters in 1948 to 1950, and especially 1953 and 1954, which caused extensive migrations of saiga on the right bank of the Volga and in Kazakhstan, promoted further dispersal of the species. On the right bank of the Volga saiga crossed the Kuma and Terek and appeared in the Sal'sk and Karanogaisk steppes and in the Cis-Caucasus. Some herds reached south as far as the Agarkhan Peninsula and crossed the ice to Chechen' and Tyulenii Islands; the southernmost point of saiga habitation there was roughly 43°39′ N lat. and the westernmost point 42° E long.; in the north saiga reached the environs of Stalingrad [Volgograd]. By 1954 to 1955 saiga had already reached the maximum possible boundaries of their distribution, spreading right up to densely cultivated regions (Dal', Gusev and Bednyi, 1956; Rak, 1956; Bannikov, 1958; Kolesnikov, 1959). In Kazakhstan at present the northern boundary has also extended significantly northward and approaches the limit prevailing in the middle of the nineteenth century. Farther northward, range expansion has been halted by land cultivation. From Ural'sk the northern boundary at present runs toward Kazakhstan station, Chilik, Orsk, and Atbasar villages, Lake Kurgaldzhin, and Kievka village on the Nura River, turning south later toward the western foothills of the Chingiztau range, and 465 from there east through the city of Ayaguz and the northern shore of Zaisan, to exit into China (Rakov, 1956; Sludskii, 1955).

In all the foregoing the northern boundary represents the limit of penetration of saiga northward in years of drought. Moreover, even in moderately wet years the area of the summer range was two or three times greater than the winter range because of access to northern regions.

Geographic Range outside the Soviet Union

Saiga inhabited Dzhungaria at the foothills of the eastern Tien Shan and, farther north, the Baitag-Bogdo range and the southern slopes of the Mongolian Altai in adjacent China and Mongolia where the nominal form was distributed (Pevtsov, 1879; Prezewalski, 1883; Kozlov, 1899; Grum-Grzhimailo, 1896 and 1914; Bannikov, 1954). Moreover, the Mongolian form of saiga today has an isolated geographic range lying in the depression of the Great Western Lakes; Khirgis-Nur, Khara-Usu-Nur, Durge-Nur, and the Khuisin-Gobi, and Shargiin-Gobi farther south. Periodic encounters of this form have been reported to the southeast, toward Lakes Biger-Nur, Bon-Tsagan-Nur, and Orok-Nur (Bannikov, 1954). In the prehistoric period evidently the range of the Mongolian form of saiga adjoined the range of the nominal form in the intermontane valleys between the Gobi and Mongolian Altai.

Quaternary finds of saiga remains outside its reconstructed range are numerous. The westernmost point of such finds falls in southern England (Pleistocene Thames; Woodward, 1890*; Reynolds, 1939; Mor [Mohr?], 1943)*. Finds have been unearthed at many places in France (Larte, 1875*; Godri, 1880*; Arselen, 1877*; Nehring, 1891*; Garle, 1891*), Belgium (Dupont, 1872*; Gasse, 1930*), Denmark (Degerbol, 1932*), Germany, and Poland (Gibsh, 1898*; Pavlova, 1906*; Kernik, 1912*, Ossovskii, 1882*; Remer, 1882*; and others).

Innumerable remains of saiga have been reported from Crimea (Gromov, 1948; Tsalkin, 1954). Some have been detected at the mouth of the Kama, on the Chagra River (south of Syzrana), north of the Little Irgiz (Pavlova, 1906 and 1933; Belyaeva, 1935 and 1939), on the southern Ural (Cherskii, 1892; Karacharovskii, 1951), at Tyumen, on the Om' River, the Ina River, in the environs of Akmolinsk, Krasnoyarsk, Nizhneudinsk (Slovtsov, 1885; Cherskii, 1891; Obolenskii, 1926; Tugarinov, 1927; Gromov, 1948; Kozhamkulova, 1957), on the Vilyui (Cherskii, 1892), at the mouth of the Olen'ok River, on the Lena and Yana Rivers, on the New Siberian Islands (Sushkin, 1925), and in Alaska (Frick, 1937*). (A.B.)

Geographic Variability

Geographic variability in saiga is almost nil, a general characteristic of steppe and desert hooved animals of Eurasia. The reasons for this are the absence of significant barriers and extensive migrations which result in a constant mixing of various populations.

Two subspecies are known. In the Soviet Union there occurs:

Common saiga, S. t. tatarica Linnaeus, 1766 (syn. *imberbis, saiga, scythica, sayga,* and *colus*). The foregoing description pertains to this form.

---

*Not in Literature Cited—Sci. Ed.

This form occurs throughout the range lying within the Soviet Union. Outside the Soviet Union it is seen in western Dzhungaria.

Outside the USSR, Mongolian saiga, *S. t. mongolica* Bann., 1946 are found. Distribution is extremely limited and they inhabit only the basins of the great lakes in northwestern Mongolia. This is a well-defined form, differing from the nominal in its generally smaller dimensions, much weaker horns, less swollen snout, and in some features of skull structure and color. (V.H.)

Biology

Population. The total population of saiga throughout their range in the Soviet Union, i.e., an area of about 2.5 million km^2, as esti-
466 mated in 1958 was roughly 2 million or a mean density of 0.8 animal per km^2. About 1.5 million saiga inhabit the Asian part of the range, covering an area of about 2 million km^2; about 500,000 animals live in an area of 150,000 km^2 on the right bank of Volga, i.e., a population density four times greater than that in Asia (Bannikov, 1958 and 1958a).

In western Kazakhstan winter congregations of saiga have been observed on the northern fringe of the Volga-Ural sands, south of the Kamysh-Samar lakes and on the right bank of Ural, where the population density has reached 14 animals per km^2. Winter congregations of saiga are known in the lower courses of the Emba, the Buzachi Peninsula, and the southern half of Ustyurt where its density is not less than 3.6 animals per km^2. One site of maximum winter congregation is the lower reaches of the Sary Su (9 to 10 animals per km^2). In the region of the Sary Su and Taidy-Monok Rivers large congregations of saiga have been reported even in summer. Massive summer congregations are also known in the Dzhilanchik River valley and in years of abundant precipitation, throughout Bet-Pak-Dala and the population density there has reached 7 or 8 animals per km^2. Significant numbers of saiga are noted regularly in winter along the southern shore of Lake Balkhash and in the Ili-Karatal and Karatal-Aksu interfluves (Sludskii, 1955).

Not much information is available about the saiga population in previous centuries, right up to the 1930's, due probably to the rapid shrinkage of its range. In the early 1930's in Kazakhstan saiga were numbered in some tens, perhaps a hundred, head. They survived individually in Dzhungaria, and only on the right bank of Volga did several hundred occur. There were hardly more than a thousand throughout the range.

In Kazakhstan a population rise was discerned in the mid-1930's, but became significant in the 1940's; by 1947 to 1948 the saiga population in Kazakhstan had already touched the level of a century ago

(Sludskii, 1955). In the territory between the Aral Sea and Lake Balkhash the saiga population in December, 1954 was roughly 700,000, with a density of 0.4 to 5.7 animals per km^2 (Rakov, 1957). There were about 900,000 animals in 1951 in all of Kazakhstan (Sludskii, 1955).

On the right bank of the Volga the population began to be restored at the end of the 1920's. In 1948 and 1949 saiga inhabited there an area of 30,000 to 40,000 km^2 and comprised roughly 20,000 to 30,000 animals, i.e., a density of about 0.7 per km^2 (Adol'f, 1950). In the next eight years the population grew tenfold; by 1950 it already equaled 100,000 and by 1952, 180,000. Mass mortality of saiga occurred in 1953 to 1954 as a result of excessive snowfall and severe winter conditions and the population fell to about 100,000 animals in the summer of 1954. However, by 1955 the animals numbered 300,000 by 1956—400,000, and by 1958—540,000 (Bannikov, 1958).

Extensive winter migrations and mass mortality occur in years of extremely unfavorable conditions; as a result the population of saiga falls sharply (as happened, for example, in 1953 to 1954). However, in subsequent years a rapid build-up of population has been recorded (Bannikov, 1958).

On the right bank of the Volga in snowy winters the majority of saiga occur in the southern part of the range, mainly in the region "Chernaya Zemlya," south of a line from Astrakhan to Elista, in an area about 20,000 km^2, where the population density reaches 10 animals per km^2. In the spring fawning period four or five sites of large saiga congregations are known—at Lake Sarpinsk, on the Kuma, and elsewhere—and the population density then reaches 10 to 14 animals per km^2. In summer, in the event of drought, saiga assemble in regions adjoining lakes and their density per km^2 may reach 10 to 12 or even 30 to 35 animals. On the right bank of the Volga over much of the year the majority of saiga generally inhabit a territory about 50,000 km^2, the population density averaging 5.2 per km^2.

467 *Habitat.* Throughout their range saiga are inhabitants of plains, positively avoiding not only mountains but also any kind of rugged terrain. They are not even found by and large among small hills, for example, sand dunes covered by vegetation. Only in winter, during snowstorms, are they encountered sometimes in hummocky sands or hilly steppes seeking refuge from the wind.

There is no doubt that saiga evolved as a species on the plains, since only there could it have developed its type of ungulate gait, an amble which ensures an exceptional speed of up to 70 to 80 km per hr but makes jumping difficult. The animal invariably attempts to run around obstacles, even insignificant ditches. Only on escaping from danger which is not clearly visible does a saiga perform a "viewing" jump upward, holding its body almost vertical. In view of the fact that saiga invariably prefer semidesert plains with compact soil, they are very fond of the fringes of large *takyrs* [clay flat]. In the event of danger the animal tries to find a *takyr* where, developing its maximum speed, it rapidly escapes its persecutor.

The height above sea level per se is not important to saiga. In the Pri-Caspian plains it lives near the sea, in Kazakhstan at a height of 200 to 600 m, and in Mongolia among lake basins located at heights of 900 to 1,600 m above sea level.

The present-day range of saiga falls within dry steppes and semideserts. Thanks to its complex vegetative associations this zone evidently represents an optimum zone for the species. Here, within relatively small territories, saiga find food in all seasons. Seasonal migrations usually do not extend beyond the boundaries of this zone. Evidently, even in past centuries, saiga have been sighted in mesophilic steppes only in years of extreme droughts (Bannikov, 1958).

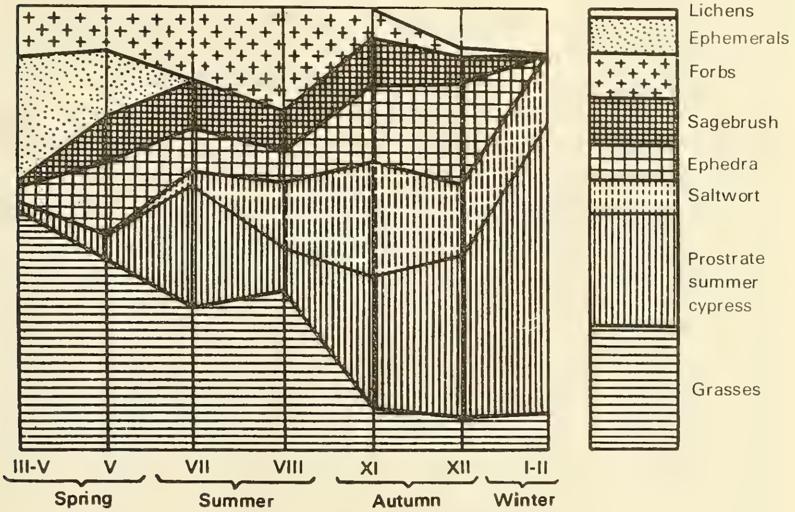
Dry steppes and semideserts inhabited by saiga, from Ergenei and the lower Volga through the whole of Kazakhstan to the edge of the Alakul' and Zaisan depressions and farther into Dzhungaria and the depressions of western Mongolia, differ widely in flora. However, plant composition everywhere remains rather similar. Drought-resistant meadow grasses (fescue, feather grass, and wheat grass) and semishrubs chiefly in the form of sagebrush, prostrate summer cypress, and pyrethrum prevail. Species of sagebrush, feather grass, and wheat grass [*Agropyron*] succeed one another from west to east. Moreover, the European-Kazakhstan semideserts are characterized by a large number of ephemerals and ephemerids, with a special abundance of rough meadow grass and often tulips. A layer of lichens often occurs on the soil. In the extreme east, in Dzhungaria and especially in Mongolia, ephemerals are absent, while sagebrush constitutes only a small percentage of the herbage. Here, in addition to meadow and feather grass, onions and saltworts (*Anabasis, Salsola,* and *Reaumuria*) predominate. In the European-Kazakh semideserts some saltworts (*Atriplex, Nannophyton, Anabasis,* and *Salsola*) may also grow here and there, giving rise to desert associations. Biomass of vegetation in saiga biotopes are not high, only 2.0 to 5.0 to 7.0 c/ha (Lavrenko, 1956).

Regions where saiga congregate for winter are usually grass-sagebrush or grass-saltwort associations, often in sandy soils. Places which saiga inhabit in summer lie within dry sagebrush-grass or grass steppes.

During snowstorms and blizzards saiga seek refuge from severely cold winds in hummocky sands and thickets of reeds, cattails, and other tall plants along banks of rivers and lakes. They avoid farms and other cultivated areas but, during intense droughts when water sources have dried up, they avidly visit plantations of edible rye, maize, Sudan grass, and other cultivated plants.

Food. The general list of plants consumed by saiga throughout their range comprises about 100 species. Many plants replace one
468 another geographically, however, and saiga in a given natural region use no more than 60 to 80 species of edible plants. About 50 such plants are known for Kazakhstan at present (Vasenko, 1950; S. Sokolov, 1951; Rakov, 1956) and about 20 species for Mongolia (Bannikov, 1951 and 1954). On the right bank of the Volga saiga consume up to 80 plant species (Adol'f, 1954; Lebedeva, 1959). The number of edible plant species in a given season does not exceed 25 to 35. This list would be even shorter if plants found rarely or in small quantities in the stomach contents of saiga were excluded. The major and commonly consumed plants number only 10 to 15, which indicates a rather restricted diet.

Of utmost importance are grasses (*Agropyrum, Bromus, Festuca, Stipa,* and *Koeleria*), prostrate summer cypress, various saltworts, forbs, ephemerals, *Ephedra,* sagebrush, and steppe lichens. The role of different species of plants and plant groups varies in different seasons (Fig. 151).



470 Fig. 151. Seasonal variations in the main foods of saiga in Kalmyk steppe (from Lebedeva, 1959).

Vasenko (1950), who studied the intake and behavior of animals in captivity, found that 12 species of plants were consumed by saiga in spring. Favorites were wheatgrass, one of the most abundant grasses on Barsa-Kel'mes Island, meadow grass, brome grass, feather grass (*Eremopyrum* sp.), *Pribrezhnitsa,* [cat foot?] (*Aeluropus* sp.), *Astragalus,* and *Ferula.* S. Sokolov (1951) found in the stomach contents of saiga caught in spring in central Kazakhstan seven species of plants, mainly grasses, saltworts, sagebrush, and lichens. Based on an analysis of spring intake, Adol'f (1954) stated that saiga on the right bank of the Volga consumed sagebrush and grasses more often than others, but avidly ate leaves of tulips, rhubarb, orache, *Statice* sp., and prostrate summer cypress. According to Lebedeva (1959) the contents of 65 stomachs examined in spring on the west bank of the Volga revealed 25 plant species. Of these, five species were primary and eight secondary. Grasses, generally not in the heading stage, constituted the main food. They were found in over 50% of the stomachs autopsied and constituted about 66% by volume of the contents. The index (K) for grasses in spring was 34.5.[92] Ephemerals occupied second place in the spring food of saiga (K, 32.4) and were found in 87.6% of the stomachs autopsied and constituted 37.0% by volume of the contents. The group of ephemerals included *Alyssum,* iris, tulip, *Gagea,* and ephemeral meadow and feather grasses. Third place (K, 13.1) was held by forbs found in 40.0% of the stomachs and constituting on the average 32.7% by volume. These three groups were followed by prostrate summer cypress, *Ephedra,* and sagebrush, the value of which did not exceed 5.0 to 7.0% (Lebedeva, 1959 and 1960).

On Barsa-Kel'mes Island 20 species of food plants have been identified in the summer diet of saiga (Vasenko, 1950). The most important are saltworts (*Anabasis* and *Salsola*), prostrate summer cypress, *Ceratocarpus,* orache (*Atriplex*), *Ephedra,* and *Aeluropus.* In Kazakhstan (Sokolov, 1951; Sokolov and Suvorov, 1955) in summer saiga feed on 19 plant species, of which *Hulthemia, Spirianthus,* licorice, camel's thorn (*Alhagi*), prostrate summer cypress, and small quantities of grasses and sagebrush are primary. In certain areas the lichen *Aspicilium* is heavily consumed. In western Kazakhstan one study at the beginning of summer revealed that the stomach contents of saiga consisted of 70 to 80% grasses. These were later replaced by prostrate summer cypress, sagebrush, *Astragalus,* and licorice (Rakov, 1956). Adol'f (1954) analyzed the stomach contents of six saiga and suggests that *Ephedra* and its berries enjoy an important place in their food, being replaced later by saltworts (*Sal-*

---

[92] L. Levedeva used the symbol "K" to express the product of percentage of finds multiplied by volume of a given food in the stomach.

sola and *Anabasis*) and grasses (wheatgrass and feather grass). Bakeev and Formozov (1955) also state that *Ephedra* and grasses (wheatgrass, fescue, and crested hair grass) represent the main 469 summer food of the saiga. Lebedeva (1959) analyzed the stomach contents of 73 animals caught on the right bank of the Volga and found that of the 23 plant species they contained the most important in summer were forbs (K, 21.5), grasses (K, 18.6), prostrate summer cypress (K, 17.3), and sagebrush (K, 12.5). All of these were found in 53 to 86% of the stomachs autopsied and constituted 17.8 to 34.8% by volume. *Ephedra* (K, 8) and saltwort (K, 5.3) also played a significant role.

In autumn, according to Vasenko (1950), saiga consume 15 plant species, among which saltworts (especially *Anabasis*), sagebrush, and camel's thorn are primary; saxaul twigs are also nibbled. In Kazakhstan saltwort (*Salsola*) and sagebrush everywhere constitute the most important autumn food of saiga; common foods are grasses vegetating for the second time and *Ceratocarpus* (Sokolov, 1951; Sokolov and Suvorov, 1955). According to Rakov (1956) saiga feed mainly on prostrate summer cypress in autumn. On the right bank of the Volga (according to an analysis of the stomach contents of 21 saiga; Adol'f, 1954) licorice occupies first place in saiga food, wheatgrass second, and prostrate summer cypress third. Adol'f considers green shoots of feather grass, lovegrass, bristle grass (*Setaria*), *Camphorosma,* and pods of toadflax (*Linaria*) ordinary food. According to Lebedeva (1959), who analyzed 53 stomach contents, the main food of saiga in late autumn is prostrate summer cypress (K, 31.9), which was found in 98.1% of stomachs and constituted an average of 32.5% by volume. Other saltworts (K, 22.5) were found in 71.7% of stomachs and constituted 31.4% by volume. *Ephedra* (K, 18.6) found in 75.4% of stomachs constituted 24.7% by volume. Next in order of predominance were grasses (K, 12.1), found in 69.8% of stomachs but constituting only 11.5% by volume, and sagebrush (K, 8.4), found in 56.6% of stomachs and constituting 14.8% by volume. Lichens were often found in small quantities in autumn food and hence their importance is low (K, 3.9) and forbs even lower (K, 2.9).

According to Vasenko (1950) saltworts (*Salsola* and *Anabasis*) and standing dead grasses are of utmost importance in winter. Sokolov (1951) found sagebrush in 60 to 70% of 20 autopsied stomachs of saiga, and saltwort *Anabasis* in 30%. In western Kazakhstan in September the stomach contents of 15 saiga comprised 80 to 90% sagebrush, saltwort, prostrate summer cypress, and camomile (Rakov, 1956). On the right bank of the Volga, according to the data of Adol'f (1954), the main food of saiga comprises wheatgrass, prostrate summer cypress, *Camphorosma,* and lichens. Bakeev and Formozov (1955) state that the main food of saiga in February is sagebrush; however, the animals avidly consume, albeit in small quantities, wheatgrass, feather grass, brome grass, and fescue. Lebedeva (1959) analyzed 29 stomach contents and came to the conclusion that prostrate summer cypress is the predominant winter food of saiga (K, 62.6); it occurred in 100% of the stomachs examined and constituted 62.6% by volume. Saltworts (K, 11.8) and lichens (K, 10.2) were of nearly equal importance and found in 79.3 and 82.7% of stomachs, constituting 15.0 and 12.4% of food volume. Often, grasses (75.8%) were found, amounting to 8.5% by volume, but their importance (K, 6.6) was low. Sagebrush was minimal in importance (K, 0.14).

Seasonal diet variations (Lebedeva's data for the right bank of the Volga; 220 stomachs covering all seasons) are as follows (Fig. 151). Grasses represent the main diet of saiga in spring, ephemerals come second place, and forbs third; shrubs and semishrubs, represented by saltwort, prostrate summer cypress, sagebrush, and *Ephedra* are of little significance. The prevailing summer food is forbs, relegating grasses to second place, with prostrate summer cypress and sagebrush increasing sharply in importance; succulent saltworts come on the list and ephemerals go off. In autumn prostrate summer cypress and succulent saltworts occupy first place, *Ephedra* also retaining much importance; the role of grasses and especially forbs is reduced, but lichens appear on the list. By winter the role of saltwort and lichens increases further, while the importance of grasses and sagebrush reduced.

During blizzards, having been driven into thickets of coastal
470 vegetation and suffering from hunger, saiga consume reeds, cattails, and other coarse food. In sand dunes they consume coarse grasses (*Elymus*) and shrubs like winterfat, tamarisk, oleaster, and others. However, all of these represent compulsory items and cannot meet the total dietary requirements of the animals.

The exploitation of pastures by saiga differs from season to season. In spring, when succulent feeds are abundant, they nibble the upper portions of plants, often only their tops. The animals select plants one to four meters apart and move rapidly through the meadow. Diet selectivity is quite distinct. With the disappearance of ephemerals in summer and considerable withering among other plants, the animals select places of more succulent vegetation, usually in low-lying areas, and consume the plants down to the ground. In that period they particularly hunt for succulent plants, for example, the berries of *Ephedra*. In autumn, when many grasses have coarsened, plants such as saltworts and licorice attract the animals by their succulence. If a second crop of grass is available, it is eaten completely by saiga. Late in autumn the young shoots of prostrate summer cypress, sagebrush, and especially grasses are also thoroughly eaten. Evidently, in their search for proteinaceous foods, beginning in autumn saiga begin to gnaw at lichens. The animals take to lichens with an even greater avidity in winter. At the commencement of spring, in thawed patches where grasses often turn green, the animals chew them down to the ground.

Saiga also eat poisonous plants not fancied by domestic cattle. Such plants comprise about 15% of the list of saiga dietary items and are found according to season in 6.8 to 67.9% of autopsied stomachs (Lebedeva, 1959).

The weight of the stomach contents of male saiga averages 3.1 kg and of females 2.2 kg, which represents 8.8 to 14% (average 9.2%) of the body weight (Lebedeva, 1959).

In spring the water requirements of saiga are fully met by the moisture present in succulent herbage and the animal usually does not visit water holes, in spite of many being present in the steppes at that time of year. The moisture content of grasses in spring is about 65 to 75% and of ephemerals 90%, i.e., the main food plants meet the total water needs of the animals.

In summer, when the moisture content of plants falls sharply, saiga select the more succulent ones. Transition to feeding on forbs
471 and later succulent saltworts and prostrate summer cypress is determined not so much by the edibility of these plants as by their succulence. Summer migrations of saigas are determined to a large extent by their search for pastures containing succulent foods. In years of drought, when the steppe is parched and succulent foods disappear altogether, saiga congregate near water holes, which become essential for their survival. In their search for water the animals often undertake considerable migrations (Bannikov, 1958).

The frequency of saiga visitations to water holes in the period of drought depends on the presence of a water source in the vicinity. Under favorable conditions the animals visit a water hole once or twice a day, in the morning and in the evening. If the water source is far away, the animal can evidently do without water for several days. Fresh water is invariably preferred to saline, but the animal may lap even salty to brackish water in extreme cases. In captivity saiga drink two to four liters of water daily. Lactating females need water most.

When drinking, saiga usually enter the water, sometime up to their belly and drink for three to five minutes, wrinkling their noses and blowing through their nostrils. The animals invariably hold their nostrils above the water surface.

Home range. Throughout the year saiga wander extensively in small or large herds and hence it is extremely difficult to identify the home range of an individual. Visual observations and data obtained by catching marked juveniles have shown that, outside the period of migrations, saiga traverse many dozens of kilometers in a few days; in the period of migrations they cover hundreds of kilometers. Females with month-old fawns have been sighted several hundreds of kilometers away from the place of their tagging (L.V. Zhirnov).

Only at the peak of rut, in December, does the male support a harem in a relatively small area of 3 to 10 km^2. However, even then the male and harem may perform migrations. In May, when newborns are not yet strong enough to move with their mothers, i.e., in the first week to ten days after birth, females stray not more than 2 to 3 km away from the site of fawning. At the end of that period females with fawns usually begin to migrate extensively (see below).

Even in the event of summer droughts, when saiga gather in regions adjoining water holes, they wander over dozens of kilometers and the temporary habitation of the herd runs into some hundreds of square kilometers.

Outside the period of migrations saiga cover several dozen kilometers every day. This distance is extremely variable and determined by the state of the pasture and herd strength. The larger the herd and the poorer the pasture, the greater the daily movement of the animals. During migrations a herd will cover 80 to 120 km or more a day, the animals moving not only during the day but also at night, feeding usually in early morning hours. A migratory herd moves in a long narrow line, while during feeding the animals scatter in a broad front.

Daily activity and behavior. In winter, as well as in early spring and late autumn, animals graze throughout daylight hours. In early summer, when it is not very hot, they graze from dawn to 7:00 to 9:00 a.m. and after a period of rest resume grazing at 4:00 to 6:00 p.m., feeding until dusk. At the height of summer, on hot days, commencing from 8:00 to 9:00 a.m. until evening, they rest, leaving the bed only around 8:00 p.m. According to the data of Lebedeva (1959), who studied weight variations of stomach contents in relation to body weight of saiga at different hours of the day, in spring the animal begins to feed in the morning and its stomach is filled to maximum by 11:00 a.m. or 12:00 noon; it feeds at small intervals throughout the day and rests at night. In summer saiga feed only at dawn and cease feeding by 8:00 to 9:00 a.m., feeding again in the evening.

In winter and spring the animal rests in depressions, often
472 among dense grass or low shrubs but on bare ground. In summer the

animals like to lie in the shade of haystacks. At night, in summer, they prefer open expanses, especially large *takyrs*. Before lying down the animal digs up the vegetation with its hooves, making a small circular bed of about 30 cm diameter. Saiga like to use for beds the mounds at ground squirrel burrows where vegetation is less and the soil soft (Fig. 154). On Barsa-Kel'mes Island, when the day is hot, saiga never lie at a given place for longer than 40 to 50 minutes, which is probably related to overheating (Vasenko, 1950).

Saiga usually move and run in their unique amble. Galloping, as usually understood, is only employed in the event of danger and jumping resorted to in order to inspect the danger better. A frightened saiga usually begins its run with such a "viewing" jump. Formerly, when pursued, saiga attempted to run across the path of the chaser in the form of an arc; now, after several years of being chased by automobiles, they still run away from any pursuer in the form of an arc, but very rarely intersect its path.

The weight load on the hoof of males varies from 700 to 833 g, on the average 741 g per cm^2; the corresponding value for females is 600 to 770 g, on the average 662 g per cm^2 (L.V. Zhirnov). The critical height of snow cover for saiga is 25 to 30 cm. It slips on ice and cannot run fast. It is a good swimmer and, in the course of migrations, crosses such rivers as the Volga. Quite often it negotiates rivers several tens of meters wide.

Vision is well developed in saiga; it can perceive danger for over 1,000 m. Olfaction is also well developed but hearing poor.

Gregariousness is highly developed in saiga when the population of the species is high; single animals are then exceptional year-round.

The lowest herd index occurs during rut, in December, when males have captured "harems" and guard them from encroachment by other males. At this time a herd consists more often of 5 to 15 animals, with a mean herd index of 9. However, even in this period juvenile males usually form herds of dozens or hundreds of animals. After rut exhausted males are usually confined to small groups of 5 to 10 animals, while the rest of the animals reform significant herds.

In summer, if the pasture is succulent and water thus ensured, a significant percentage of the population scatters throughout the steppe in groups of 5 to 9 to 15 animals. Part of the population, after weaning, nevertheless remains in large groups. Thus the mean herd index in summer is 30 to 40. The following results were arrived at by analyzing encounters of over 100,000 animals during aerial surveys (1950 to 1958) and automobile counts (1957 and 1958) from May through September in Kalmykiya: most frequently encountered were herds of 10 to 50 animals (30 to 40%), 1 to 5 animals (20%) less commonly groups of 5 to 10 or 50 to 100 animals comprised about 15%, and herds of 200 to 500 animals were relatively rare (2.0 to 3.0%), and the percentage of encounters of herds comprising over 1,000 animals was again larger (8.0 to 9.0%) (A.G. Bannikov). During aerial counts in Kazakhstan it also was found that herds of 30 to 40 animals were most common (Rakov, 1957).

Even within large congregations of saiga (when they are not in motion), individual herds of 5 to 50 animals can always be identified. When agitated or migrating animals commence running, such individual herds will gradually merge and form a dense front several dozens of meters wide and, on occasion, even a hundred meters wide. Furthermore, the animals behave as members of a single herd independent of their numbers. Leaders are not apparent in such a moving front, covering sometimes the entire horizon and consisting of many thousands of animals, nor can they be distinguished in small herds. Harems constitute an exception.

Seasonal migrations and transgressions. Saiga wander incessantly, but regular seasonal migrations are not a characteristic phenomenon of all populations. They neither occur every year nor take
473 place in every region. Seasonal migrations of saiga have not been recorded in Mongolia. In years of moderate wetness and snow a goodly percentage of the population has invariably settled in several regions of Kazakhstan and on the right bank of the Volga. In years of poor snow and excessive summer precipitation the animals may be found year-round throughout their range (Adol'f, 1950; Kolesnikov, 1950; Rakov, 1956; Bannikov, 1951, 1954 and 1958).

Saiga do not exhibit a preference for a dual range—one for spring-summer and the other for winter (Bakeev and Formozov, 1955). Nevertheless regions of seasonal congregations have been detected in three periods: winter, spring, and summer. Corresponding migrations also take place. Winter gatherings usually form at places of minimum snow thickness. On the right bank of the Volga this region falls south of the line Astrakhan-Khalkhuta-Elista. In Kazakhstan it covers the lower reaches of the Sary Su River, the edges of Volga-Ural sands, the left bank of the Ural, and several other places. Regions of winter gatherings vary in different years, depending on the prevailing snow cover. On the right bank of the Volga in years of negligible snow cover (for example in the winter of 1957–58) winter congregations of saiga shift time and again from Sarpinsk lakes in the north to Chernaya Zemlya in the south and back. Such migrations of winter saiga congregations within summer habitats, or only an insignificant winter shift into the southern half of summer habitats, also occur in Kazakhstan (Rakov, 1956). It should be emphasized that even when winter congregations of saiga form in the southern parts of their range, the animals still change from one pasture to another and move constantly in extremely divergent directions.

The periods and intensity of autumn–winter migrations of saiga depend on atmospheric conditions prevailing in a given year. Usually gradual migrations to wintering areas occur at the end of September to October, but often only in December–January or even in February. By the middle of April saiga are mostly in fawning sites. In severe winters massive autumn and spring migrations occur in central Kazakhstan, from the southern regions of Bet-Pak-Dala to the north and back within a very short period (Sokolov, 1951; Sludskii, 1955).

Summer congregations depend on the frequency and distribution of summer precipitation, which determines the state of pasture and the availability of water sources to meet the requirements of saiga. Distinct summer congregations are seen in years of drought when saiga migrate to more luxuriant pastures and water holes. Such regions are mostly located in the northern parts of their range and also in a broad belt along rivers and lakes. During the course of summer such sites of saiga congregations keep changing, depending on the rainfall in a given region.

Summer migrations coincide with the period of drying up of grasses and water sources. These periods are extremely variable. Thus, in the droughty summer of 1957 such a migration to the western bank of the Volga commenced early, in the middle of May. According to the data of L.V. Zhirnov saiga began moving southwest from fawning sites in the northeastern part of the right bank of the Volga. The wandering herds covered a large area. According to visual calculations this area measured about 300 km^2, while the population of migrating saiga was 150,000 to 200,000. It was impossible to distinguish one herd from another. The congregation consisted roughly of 90% females with fawns and advanced at 5 to 10 km per hr. Some groups of animals stopped in saucer-shaped depressions still green with grass. The entire steppe swarmed with saiga from end to end. The bleats of tens of thousands of fawns and the responding calls of the mothers could be heard as a rumble for quite some distance; a dust cloud hung over the herd. The wandering herd covered 200 to 250 km in 8 days. In this same period, or a few days later, smaller assemblies of several thousand, comprising mainly males, similarly moved across from east to west. In the northeastern Pri-Caspian lowland some small, isolated herds remained behind

474 but their total number was only several hundred. The new sites to which these saiga migrated (Manych steppe and Ergenya) differed from the previously occupied sites (northeastern Pri-Caspian lowland) in the availability of more succulent pastures. Pastures were quickly depleted, however, and in about a month's time the animals were on the move again, but not as eagerly as before. Part of the herd advanced farther west but on encountering densely populated regions and cultivated farms there, quickly changed course northeast. Other herds moved straight east and northeast to the Sarpinsk lakes. There, in early July saiga congregations numbered 100,000 to 120,000. After the rains, in mid-July, saiga abandoned the then intensely depleted pastures and dispersed extensively in the steppe. Similar migrations, but on a smaller scale, were seen in the summer of 1957 in the southern part of the steppe also.

The summer of 1958, characterized by excessive precipitation, was altogether different on the right bank of the Volga. Luxuriant and succulent pastures and water in lagoons and shallow lakes throughout the steppe determined the distribution pattern. Solitary females with young and small herds consisting of five to seven to nine animals could be seen everywhere. Large groups numbering 100,000 to 150,000 animals, seen in the period of calving in the northwest (in the Nikol'sk region), migrated by the end of May to south of the Sarpinsk lakes. Saiga from this group partly scattered, as confirmed by the presence of young tagged at the site of birth, far away in the south in July (Yashkul'). During June the remaining part of the herd advanced far south, reaching the Khalkhuta region in early July, where there are no permanent water sources. There, moving sometimes northwest, sometimes south, and sometimes again north, the animals spent the entire summer wandering far from rivers and large lakes in an area of about 20,000 km^2. Another congregation of saigas consisting of 30,000 to 40,000 animals remained in the south, in Chernaya Zemlya (east of Adyk). Similarly, small herds of saigas spent the entire summer on the right bank of the Kuma River.

Similar phenomena are known for Kazakhstan where, in wet years, the animals were confined throughout summer in wintering sites, migrating only in the event of local droughts into regions in which there were rains. On the other hand, in years when large areas were affected by drought, significant congregations of saiga approached the river banks or left their normal habitats, migrating north. This occurred, for example, in 1946 and in 1951 when herds approached the Saratov-Aktyubinsk railway line and stray animals were seen even north of this line (Rakov, 1956). Hence summer migrations represent an irregular phenomenon and are wholly determined by the conditions of water holes and pastures.

Spring congregations are seen in the period of calving. They are not confined to the southern or northern parts of the range and occur everywhere. However, the sites of these congregations are more fixed than those of summer and winter groups. Migrations of saiga into these areas occur gradually, usually from end of March to end of April. Prolonged snowstorms leading to the formation of a continuous and high snow cover, frozen grounds, intense drought over large areas, steppe fires, and other natural calamities contribute to nonperiodic migrations of saiga.

The range of saiga is confined within the semidesert where the snow cover usually does not exceed 20 to 25 cm, and more often 10 cm, so that the animals can easily obtain food. Moreover, the uneven snow cover in semideserts (as a result of snow being blown by wind into lowlands and melting rapidly in wet *solonchaks* [saline soil area] renders pasture accessible to the animal throughout winter. However, in some winters heavy snowfalls accompanied by strong winds and temperature drops cause a food deficiency. In Kazakhstan and on the right bank of the Volga such conditions recur once in 10 to 12 years (Sludskii, 1955); in such unfavorable years saiga migrate in diverse directions to varying distances. In the severe winter of 1953–54 most of the saiga on the right bank of the Volga migrated
475 south, as a result of which their range on the right bank of the Kuma enlarged suddenly; some moved onto the ice of the Caspian Sea, some crossed over to the left bank of the Volga, and some migrated west. It was during severe winters that saiga transgressions were seen over maximum distances: some herds reached the Sulak River in the south and were seen on Tyulen and Chechen Islands (Bakeev and Formozov, 1955; Dal', Gusev and Bednyi, 1956; Rak, 1956; Rakov, 1956). On the contrary, in the winter of 1949–50 during snowstorms the majority of saiga from Chernaya Zemlya migrated north (Lavrovskii, 1950). During such migrations they traveled in a leeward direction and covered 100 to 120 km or more per day. In search of protection from the wind and a source of food, the animals reached sand barkhans and thickets along the banks of rivers and lakes and many perished (see below).

Frozen grounds and thick snow crust also obstruct access to food (Vasenko, 1950) and saiga migrate from such regions as, for example, occurred in 1951 in the Ural-Kushum interfluve region (Rakov, 1956). Probably an abundance of blood-sucking insects and steppe fires also lead to migrations from one region to another (Rakov, 1956). Regardless, migrations caused by natural calamities are not in the nature of regular migrations with respect to time or to direction of movement of saiga.

There is no basis for assuming that saiga undertook regular seasonal migrations in the past. The observations of Pallas (1773), Rychkov (1762), Eversmann (1850), Glitsch (1865), and Tolstoi (1906) only indicate that saiga in droughty years penetrated north nonperiodically right up to feathergrass steppes. Consequently, the boundary of saiga distribution in the thirteenth to the nineteenth centuries shifted farther northward, compared to their present-day range, and actually does not represent the boundary of permanent summer habitation of the species, but only the limit to which the animal reached in some years of intense drought. Thus, cultivation of virgin northern lands on the right bank of the Volga and also in Kazakhstan only led to a reduction of sections inhabited by saiga in drought periods.

In spite of the absence of regular seasonal migrations, saiga are constantly on the move. These migrations are determined by the above-listed factors, among which the most important are state of pasture and access to food and water holes. The great mobility of saiga often creates the impression of regular migrations.

Reproduction. Saiga are polygamous. On the west bank of the Volga the mating season commences in the last few days of November and ends around December 20, i.e., it extends for a little less than a month. Mass mating in the Kalmyk steppe occurs between the 15th and 25th of December and continues for about 10 days. In Kazakhstan these periods shift 10 days later and another 10 days in Mongolia; thus from west to east there is a gradual delay of the breeding season (Bannikov, 1958).

Mass mating is preceded by the process of "harem" formation. The male gathers a herd of 5 to 10 females and protects them from encroachment by other males. The number of females in a "harem" depends on the strength of the male and the sex ratio in the population and may reach 40 to 50 females. The male holds his "harem" in a small area, usually on level ground; here the snow is trampled over a radius of 30 to 80 m and innumerable beds, urine spots, and broken and trampled vegetation are seen. Corpses of unsuccessful rivals are not uncommon.

In the mating season an intense secretion of abdominal and suborbital integumental glands occurs in males. The animals are covered with these secretions, foam from the mouth, and sometimes even bleed from wounds sustained during fights. Mating takes place at night; males rest for long periods during the day. Fights between males are extremely violent and sometimes end in the death of one

rival. During rut males almost do not graze but often eat snow. They lose caution and even attack men. In this period they become
476 extremely emaciated, weakened, and often become an easy prey to predators, or perish in severe winters. Male mortality in this period can reach 80 to 90% (Sludskii, 1955; Rakov, 1956).

Most females mate for the first time at the age of seven or eight months and give birth to their first fawn at the age of one year. The statement that females mature at the age of 20 months (Sludskii, 1955) is erroneous. Males come into rut for the first time in their second year.

Gestation among saiga lasts five months; according to data collected in zoological gardens it is about 145 days. The first fawns are seen on the west bank of the Volga in the last few days of April. Mass fawning occurs there in the first week of May, in western Kazakhstan in the middle of May (Rakov, 1956), in central Kazakhstan in the last 20 days of May (Sokolov, 1951), and in Mongolia at the end of May for 6 or 7 days. Some individual females may fawn in the last few days of May (Kalmykiya) and up to early June (Kazakhstan).[93]

Small groups or individual females in parturition can be seen throughout the range. The majority of pregnant females gather at some definite places, however. Such regions of large congregations are known at some places on the west bank of the Volga and in Kazakhstan and are relatively fixed. For several consecutive years in the 1940's a congregation of saiga was observed on the right bank of the Volga in southern Stalingrad [Volgograd] district and in the Bol'shoi Tsaryn region (Lavrovskii, 1950; Adol'f, 1954). In 1957 the main part of this congregation migrated several dozens of kilometers southeast of their former site, and even more eastward in 1958.

The sites of mass fawning of saiga are located in open plains with some saucer-shaped depressions. Vegetation in such places is usually extremely sparse, consisting of sagebrush, grass or saltwort semidesert. Plains are preferred by females at the time of fawning so that they can spot danger a long distance away. Sparse vegetation with bare spots in which the animals can lie render the females and fawns invisible because of concealing coloration. A resting fawn or female is difficult to spot on clayey soil even at a distance of a few steps. Only a few females fawn in rugged terrain or among dense, tall herbage (Bannikov, 1958).

The places selected by females for fawning are usually far removed from human habitats and deep inside semideserts. The quality of pasture is seldom very good, which is probably the reason for the rapid departure of females as soon as fawns become strong enough to trail behind them. The proximity of a water hole is not essential. Saiga collect in the northern Kalmyk steppe at a distance of 30 to 40 km from the nearest source of water (Lake Sarpa). Occasionally small groups of females fawn in fields; newborns were detected in the Kalmyks steppe in 1957 and 1958 among plantations of edible rye and Sudan grass.

---

[93] A pregnant female with a fetus already covered with hair was caught on November 30, 1957 in southern Stalingrad [Volgograd] region.

Fawns very rarely lie among dense grass and are usually found on the bare ground, on mounds around the burrows of ground squirrels, or in the regular circular beds of adult animals. The mother usually makes no special "delivery pit".

The density of females at fawning sites varies but is usually very high. In the northern part of the Kalmyk steppe, in 1957 in the region of Alata-Burata, about 30,000 to 50,000 animals were found in an area about 100 km^2, or 3 to 5 females per hectare. Some males were also present but their number did not exceed 2 or 3% of the total population. In the Pri-Kum steppes, west of Bakres, the density of females gathering for fawning in 1954 was 30 animals per hectare. In 1955, between Adyk (Yuzhnyi) and Chernozemel'skoe there were some tens of thousands of saiga in an area 900 km^2 (Dal', Gusev and Bednyi, 1956).

477 In the northern part of the Kalmyk steppe in 1957 and 1958 newborns lay in groups of 2 to 5 to 8 animals 10 to 20 m from each other with 100 to 200 m between groups. Lone fawns were encountered rarely. The density of fawns varied from 0.3 to 4.0 animals per hectare; the mean density may reach 5 or 6 per hectare however (Bannikov, 1958).

Such aggregations and densities of fawns evidently do not occur in Kazakhstan. Rakov (1956) found that females most often gathered for fawning in groups of 15 to 20 animals and sometimes 150 to 200 animals. Fawns lay at distances of 100 to 300 m from each other. A large congregation of fawning females was once observed in Bet-Pak-Dala (Kul'pin, 1954).

On the average two-thirds of the females bear twins. In Kazakhstan 70 to 90% of females deliver twins (Vasenko, 1950; Sokolov, 1951; Sludskii, 1955; Rakov, 1956). Twin fetuses were found in 73.8% of 293 females older than one year, and only in 5.0% of 140 females aged up to one year, autopsied in the winters of 1958 and 1959 in Kalmykiya; correspondingly, 26.2% of the older females and 95.0% of the younger ones had only a single fetus. Not a single female contained three fetuses. Among 14,000 fawns examined in 1957 and 1958, there were only four instances of three fawns lying together

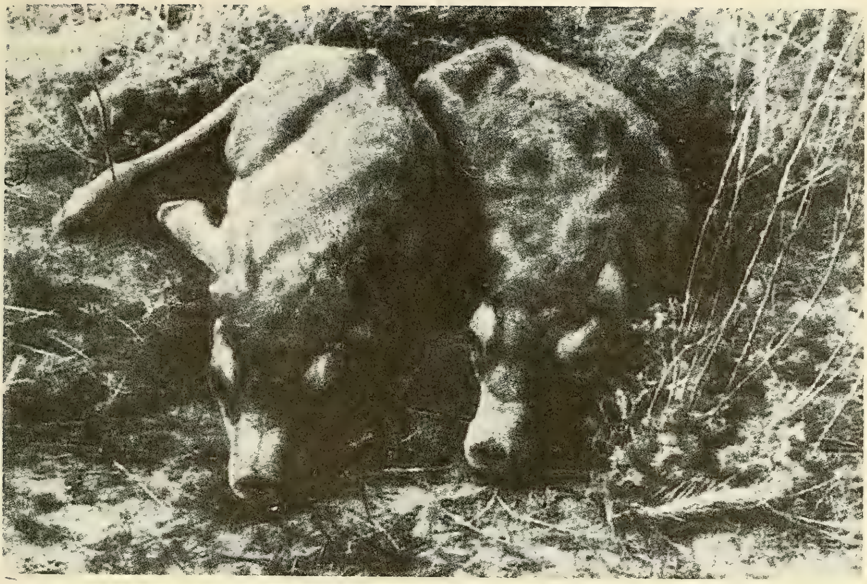


Fig. 152. Newborn saiga fawns in the Kalmyk steppe. Photograph by A.G. Bannikov.

(A.A. Fandeev). In Bet-Pak-Dala only two of 164 gestating females carried three fetuses (1.2%) (A.A. Sludskii).

All of the investigators who have autopsied females in winter have reported barrenness as a rare phenomenon. In the data given above 4.0% of the older females and 15.0% of the younger ones were barren (A.A. Fandeev).

Delivery requires a few minutes to an hour or more. In nature the entire birth process is quite often over in 15 to 20 minutes. Some hours before delivery the females lie down and stand up several times. The female moves away immediately after delivery.

Growth, development, and molt. In the first few days after birth saiga fawns lie in an immobile posture much of the time and get up only when hungry, which is usually twice a day—early morning and
478 evening. Fawns have actually been seen standing up in the evening, running and bleating to waken their mothers; some approach man or an automobile and trustingly extend their neck. The mother standing at a distance of 200 to 250 m becomes restless and jumps around. According to Adol'f (1954) females feed the young twice or thrice a day. Feeding of fawns moving with their mothers has been recorded for every 20 to 30 minutes throughout daylight hours (A.A. Fandeev).[94]

---

[94] These and the following observations, unless otherwise stated, pertain to the right bank of the Volga.

Right from the very beginning fawns spend the night alone and mothers come to feed them in the morning when the sun is already high, around 8:00 to 10:00 a.m. Each female feeds, evidently, only her fawn or fawns. Females have actually been observed running among fawns and calling to their offspring. Many fawns responded to this call but the female paid no attention until she found her own offspring.

At the age of four to eight days fawns begin to nibble grass. In June milk is invariably found to the same extent as pasture food in the stomachs of fawns. In July small amounts of milk are found in the stomachs of fawns caught early in the morning and evening. By August most fawns have taken wholly to pasture food; only a few females continue to suckle. However, females caught in August still had milk in their mammary glands. Thus the period of lactation continues for 4.0 months but the young actually survive mainly on milk for not more than 2.0 to 2.5 months.

For the first three or four days after birth fawns lie down continuously and only when already finding themselves held by man do they attempt to break loose and cry out. They can run at the end of the second day but tire quickly and soon lie down. Older fawns run away with the speed of a hare on the approach of man. The young trail behind their mothers on roughly the tenth day.

Newborn fawns (based on data for 45 males and 45 females) weigh 2.0 to 4.4 kg with an average of 3.5 kg; their head-body length varies from 53 to 67 cm with an average of 60 cm; males are 200 g heavier and 2.0 cm longer than females (A.A. Fandeev). On Barsa-Kel'mes Island the weight of newborn male fawns averaged 4.62 kg and females 3.85 kg; their [head-] body length was respectively 65.9 and 64.5 cm (Vasenko, 1950). In Kazakhstan the weight of newborn fawns (based on data for 23 animals) was 3.9 to 5.2 kg (Sludskii, 1955). Compared to adults fawns have long legs, ears, and tail, but their nasal proboscis is poorly developed.

At the age of one month saiga fawns weigh 6.0 to 9.0 kg and measure 70 to 80 cm in body length[95]; at two months their weight increases 2.5 to 3.0 times in relation to the initial weight and the body length increases by 1.5 times. At six months males weigh 18 to 27 kg (average 24.5 kg) and females 16.0 to 24.5 kg (average 23.kg); their body length is correspondingly 109 and 107 cm. At the age of one year males weigh an average of 28.0 kg and females 24.2 kg; their

[95] The statement that females grow more rapidly than males (Adol'f, 1954) is evidently erroneous and occurred because the sample was too small and pertained to fawns raised in captivity.

body length is correspondingly 116 and 110 cm. The growth of females ceases by the age of 20 months while males continue to grow for two years. From the moment of the onset of her first pregnancy (seven or eight months), a female ceases growth and recommences development only in July at the age of 14 months when lactation is over.

Small horns in the form of black cones about 1.0 cm long are visible under the skin of males roughly at the age of one month. By six months they are 10 cm long but still black. In the seventh or eighth month the black skin cover is gradually shed, commencing from the tips, and the horns turn lighter in color by the age of 13 or 14 months. At the age of one year horns measure 17 to 23 cm (average 18.6). Horn growth ceases roughly at the age of 20 months, when their average length is 32 to 33 cm.

479 Adult males in Kazakhstan in December weigh 37.4 to 60.0 kg with an average of 45.7 kg; females weigh 34.0 to 37.3 kg with an average of 36.0 kg (Sludskii, 1955). On Barsa-Kel'mes Island males weigh an average of 37.3 kg and females 30.5 kg (Vasenko, 1950). In the Kalmyk steppe the average weight of males in December is 42.4 kg and in April 36.1 kg; females correspondingly weigh 33.5 and 29.1 kg. At the end of the period of rut males lose a third or more of their former weight.

At birth fawns have all three pairs of milk incisors, two pair of milk canines, and three pairs of milk premolars in the upper and lower jaws. The premolars attain full growth at two months of age. Moreover, newborn fawns have a pair of rudimentary canines on the upper jaw, located on the line of the joint of the jawbone and the premaxilla; these disappear roughly around the end of the first month. Commencing from the second month permanent molars begin to cut through and attain their maximum size at the age of 17 to 18 months. However, the masticatory surfaces of the last upper molars (m^3) are fully formed only in the third year.

The replacement of milk teeth with permanent premolars commences at the age of 12 to 13 months and is completed in the 15th month. The replacement of milk incisors and canines commences from the middle incisors at the age of 13 to 14 months and ceases at 20 to 24 months when the canines are replaced (A.G. Bannikov and A.A. Fandeev; Khusainov, 1959).

The age of saiga fawns up to two years can be established from the extent of replacement of deciduous teeth with permanent ones; age up to three years can be established from the extent of formation of the masticatory surfaces of the molars. Age over three years can only be estimated from the extent of wear of all teeth, especially of the incisors.

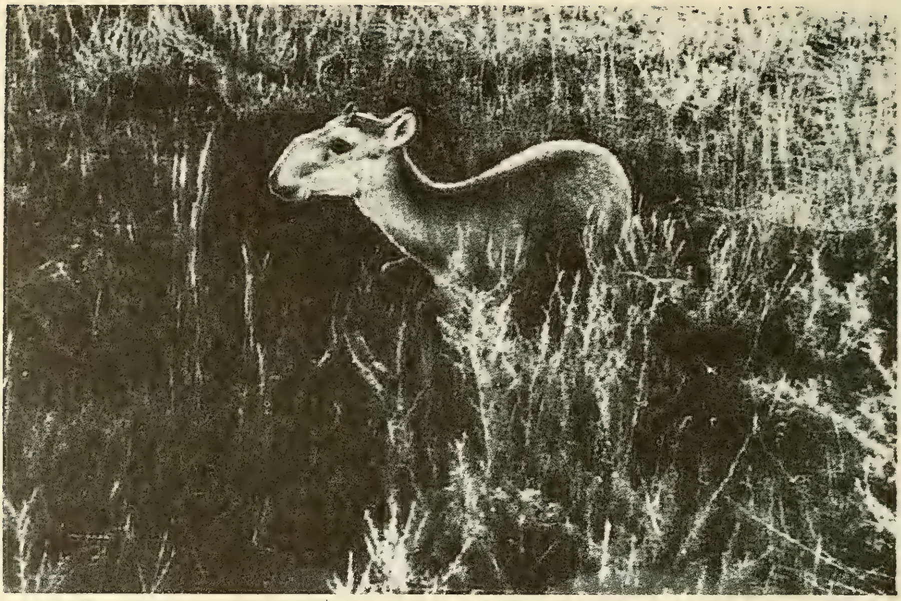


Fig. 153. Two-month-old male saiga fawn. Photograph by A.G. Bannikov.

Longevity of saiga in nature is not known. Males not less than five to six years old and females twice that age have definitely been established.

Roughly at the age of two weeks fawns commence their first partial molt. The juvenile, slightly curly wool is shed and the summer coat of the adults develops. This molt is greatly extended in time and ceases at the end of July or early in August.

480 Spring molt commences in early, middle, or end of April and continues for 20 to 30 days, i.e., until early or middle of May. In the eastern part of the range molt commences 10 to 15 days later than in the west. Molt depends on the course of spring. The first to fall is the hair at the end of the snout, around the eyes, around the lips, and on the inner surface of the distal portions of the limbs. Molt later extends to the upper surface of the snout, forehead, and back; this is followed by molting of the flanks, neck, abdomen, and exterior of the proximal portions of the limbs.

Autumn molt commences in the last few days of September (in the east) or early October (in the west) and continues to the end of November or early December, i.e., for about 2.5 months. The young commence molt later than adults. In autumn the first to molt is the wool at the tip of the snout, on the hips over the tail, and on the inner surface of the legs. Molt then extends to the forehead, rear of the back, and lower surface of the neck. The posterior part of the back, flanks, and neck molt next, while the abdomen and outer suface of the legs molt last.

Enemies, diseases, parasites, mortality, competitors, and population dynamics. Wolves are the primary enemy of saiga. The distribution of wolf within the range of saiga is distinctly correlated with the distribution of the latter. In regions of summer and winter congregations of saiga the wolf population is invariably high. A solitary wolf cannot chase an adult saiga, but males emaciated in the period of rut, females before calving, and newborn fawns are killed in very large numbers. Wolves successfully chase saiga when the snow cover is deep, since the weight load on the tread of saiga is roughly 4.5 times greater than that of wolves. According to Rakov (1955) wolves usually hunt in packs; some chase saiga while others block its path, which invariably is circular. Rakov also thinks that in Kazakhstan wolves destroy up to 20 to 25% of the total saiga population. On the right bank of the Volga where the wolf population is presently very low, they do not play a significant role in the destruction of saiga. This is one reason for the particularly rapid rise of the saiga population in this part of their range.

Adult saiga have no other enemies. Red foxes attack newborn calves but much of their quarry consists of the carcasses of the young. Steppe eagle, golden eagle, and raven represent enemies of newborn fawns. Black kite, crow and black and griffon vultures, evidently consume only dead fawns. Probably the corsac fox eat only carcasses. Stray dogs inflict considerable damage on newborn fawns.

Females protect calves from predatory birds by jumping up and attempting to strike the predator with their head or forelegs. Females exhibit a similar protective reflex toward a low-flying airplane.

Among the diseases affecting saiga the most common is hoof-and-mouth disease, which has led sometimes to mass mortality. Characteristic short horns are seen in males suffering from hoof-and-mouth disease because the terminal portion falls off. Epizootic diseases are known on the right bank of the Volga and in Kazakhstan; they arise as a result of the contact of saiga with sick domestic cattle (Skorin and Shubin, 1958). There are references, inadequately substantiated, to saiga suffering from braxy, cattle plague, and Siberian ulcers. Saiga suffer from brucellosis but very rarely spontaneously; there is no basis whatsoever to consider saiga a source of brucellosis infection (Kotlyarova, Taran, Zamakhaeva, Chekomasova and Polyakova, 1957; Uralova, Isakov, Gubina and Shapovalov, 1957; Shiryaev and Shapovalov, 1956).

About 35 species of parasitic worms have been identified in saiga. Twelve species are found in animals of Bet-Pak-Dala and Barsa-Kel'mes Island (Sokolov and Boev, 1950). Of utmost pathogenic importance are *Skrjabinodera saiga* and *Parafilaria antipini*. In Kalmykiya 23 species have been detected, of which 19 are nematodes and 4 cestodes. Saiga are particularly vulnerable to *Skrjabinema ovis* and *Trichocephalus skrjabini* (Yu.P. Golubovskii). Coenurosis (Tarasov, 1955) and blindness as a result of telasiosis are known; the patho-
481 genic importance of other species has not been clearly established. The coccidian *Eimeria elegans* has been detected (Svanbaev, 1956). Among ectoparasites, the louse *Linognathus sanguineus* (Bezukladnikov, 1957) and the mites *Hyalomma scupense, H. plumbeum, Dermocentor pictus,* and *Rhipicephalus sanguineus* are quite common (Kondrashkin, Kukin and Kozin, 1955; Dal', Gusev and Bednyi, 1958). In some regions saiga suffer from blood-sucking dipterans, especially horseflies (Tabanidae), which may cause migrations into areas far away from water sources during the hours of intense flight of horseflies (Olsuf'ev and Formozov, 1953), or cause the animals to abandon altogether regions adjacent to water sources (Rakov, 1956).

In the past, until the end of the nineteenth century, saiga suffered intensely from a species of skin gadfly (*Pallasiomyia antilopum*), whose larvae occurred in large numbers under the animal's skin and engendered restlessness and emaciation (Porchinskii, 1902). At the

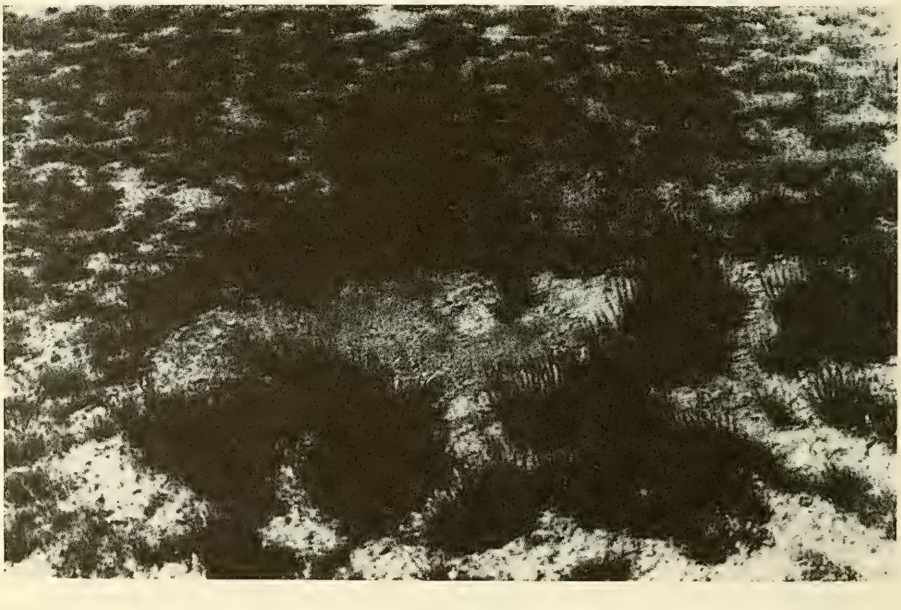


Fig. 154. Bed of a saiga. Kalmyk steppe. Photograph by A.G. Bannikov.

end of the 1920's, when the saiga population decreased sharply, the skin gadfly parasitizing them evidently became extinct, since it has not been detected in saiga from the 1930's to date. *P. antilopum* has been found only in some isolated populations of Mongolian saiga (Grunin, 1957).

Saiga have no serious competitors among wild animals. Occasionally voles (common and lemming) [*Microtus arvalis, Lagurus lagurus*] and goitered gazelle become competitors in periods of drought.

Among natural calamities snowstorms continuing for several days cause not only mass migrations of saiga (see above), but also lead to the death of a large number of animals. Mass mortality was observed, for example, in the winters of 1949 to 1950 and 1953 to 1954 on the right bank of the Volga (Lavrovskii, 1950; Dal', Gusev and Bednyi, 1956; Rak, 1956). In the winter of 1953 to 1954 about 80,000 saiga perished. In these same years and in the winters of 1948 to 1949 and 1950 to 1951 *dzhut* occurred in Kazakhstan, as a result of which the saiga population shrank by half. In the last hundred years nine winters of particularly intense *dzhut* have occurred, causing mass mortality among saiga (Sludskii, 1955). Frozen grounds and thick snow crusts also lead to the death of saiga due to want of food, and animals with injured legs become easy prey for wolves. What-
482 ever the calamity, the first to perish in winter are adult males emaciated in the period of rut, followed by juveniles under one year (see below).

Early droughts occurring simultaneously over large territories may lead to the death of saiga, especially juveniles and lactating females, due to scarcity of water (Levrovskii, 1950; Adol'f, 1950). Deaths of saiga mired in drying lakes have been recorded.

Thanks to high fertility and the exceptionally early onset of maturity in females, a rapid restoration of the population is characteristic of saiga. Another characteristic feature of their population dynamics is that in a short period (in the event of a fairly high total population), even under natural calamities the population decreases by one-half to one-third. Since the animal is highly mobile a significant part of the population invariably moves away from such calamities (Bannikov, 1959).

About 80% of the fawns survive up to August since 1.3 to 1.4 fawns per female have been recorded in that month versus 1.6 at the time of birth (counts made in the Kalmyk steppe over six years). In winter, after estrus, in which year-old females also participate in mating, adult males emaciated in combat die in such large numbers that by spring they constitute only 10 to 15% of the total population and only 3 to 5% in the event of a severe winter (Sludskii, 1955; Rakov, 1956; Adol'f, 1954). However, this causes no significant loss to the population since saiga is a polygamous animal and the sex ratio at birth is 1: 1. Thus in 1957 out of 3,905 newborns, male fawns numbered 1,955 (Bannikov, Zhirnov, Lebedeva and Fandeev, 1959); in 1958 of 8,165 fawns, males numbered 4,239 (A.A. Fandeev). These features also determine the characteristic population dynamics of saiga, which evidently has no parallel among other ungulates.

Field characteristics. In spite of a somewhat heavier build than gazelle, saiga are fleet-footed. During its unique "amble," generally employed when running, the animal bends low, dropping its head almost to the ground, and moves rapidly at a constant speed without vertical movements of the torso. Thus saiga are readily distinguished from gazelle even at some distance. In winter, when there is no snow, saiga appear pure white from a distance; broad gray streaks on the neck are present only in males.

483 The hoofprint of an adult saiga is about 60 to 70 mm long and 45 to 55 mm wide, and larger with a blunter anterior end in males than in females. It is clearly differentiated from that of a goitered gazelle by its larger size, greater width, and circular form. Furthermore, the hoof of a standing saiga is more or less separated, so that the print always has a groove at least for the forelimbs, on soft ground this groove is in the form of a furrow dividing the hoofprint longitudinally into two parts (Fig. 155).

Saiga fecal pellets are larger than those of goitered gazelle, reaching 11 to 14 mm in length and 9 to 11 mm in thickness.

At places where saiga live circular beds on the mounds of ground squirrels or on bare sections of the soil are quite common. Tracks and innumerable trails are invariably seen near water. In herds containing juveniles the call of fawns and females is invariably heard. The voice of the former resembles the bleating of lambs, while females emit a short, hoarse "kee". Males call intermittently in a low voice or even growl. (A.B.)

Economic Importance

Hunting saiga is known from very early times. In the eighteenth century collective hunting already prevailed and saiga horns were bought for export to China at a high price (Pallas, 1778). According to the data of Nebol'sin (1855), from 1840 through 1850 Bukhara and Khiva buyers took to China 344,747 pairs of saiga horns. Every year 11,000 to 61,000 pairs of horns were exported from the Kirgiz steppe during the years 1853 through 1860; exports from Aleksandrov Fort

482 Fig. 155. Tracks of saiga on the shore of a lake. Photograph by A.G. Bannikov.

totaled 543 to 5,493 pairs (Meier, 1865). Between 1857 and 1861 Petropavlovsk customhouse cleared 7,719 to 41,720 pairs of horns annually (Krasovskii, 1868). According to Borodin (1891) in the last quarter of the previous century saiga hunting represented one. of the most profitable occupations of the local populace in Pri-Ural steppes. According to Silant'ev (1898) hundreds of thousands of saiga were caught annually in Russia at the beginning of the nineteenth century.

The most prevalent methods of hunting were chasing the animals into an ambush, lying in wait at water holes, or using pens made of cut reeds. In the latter the herd was either chased into a section of cut reeds or reed fences set up. Clumps of earth were placed at some distance from each other to form two long, converging lines. Something like a funnel with a mouth width up to 5 km was thereby formed. At the narrow exit from the funnel sharp reed stalks or spikes 70 cm high were driven into the ground. The saiga herd emerging from the funnel neck at great speed fell on the sharp spikes, which pierced their chests or slit their abdomens. This barbaric method was used with minor variations in Kazakhstan and Kalmykiya (Levshin, 1832; Vitte, 1856; Dal', 1836; Avdiev, 1858). In the lower reaches of Chu River this method, called "aran" in Kazakhstan yielded up to 12,000 saiga per day. Thousands of those which escaped were mutilated (Sludskii, 1955).

Saiga were also chased on smooth ice on which the animals are helpless. Pits were dug and traps laid in trails to water holes or the animals caught with the help of golden eagles (Konev, 1858; Mozer, 1888). Killing was done year-round but mostly in summer and in winter during snowstorms. Meat, hide, and horns were used. A Kazakh hunter caught up to 40 to 60 animals every year (Rakov, 1956).

Saiga hunting was totally banned in 1919. The rapid growth of the population in the 1940's permitted licensed hunting to be introduced in 1951 on the right bank of the Volga and in 1954 in Kazakhstan. In 1951 on the west bank of the Volga licenses were issued for 10,000 saiga; however, about 200,000 animals were killed in the next five years. In Kazakhstan in 1954 licenses were issued for 50,000 animals and in 1957 for 100,000. The Astrakhan' Hunt-utilization Organization (*Promkhoz*) organized in 1956 controlled the hunting
484 of saiga on the right bank of the Volga; it also organized the conservation of saiga and implemented effective measures. In 1956 the *promkhoz* caught 106,000 animals, in 1957—128,000, and in 1958—200,000.

Teams of hunters hired by the *promkhoz* hunt during the day by chasing a herd into a network of concealed riflemen. In hunting at night automobiles cruise at a speed of 15 to 20 km per hr; each unit has a team leader or "torch bearer" and two or three marksmen. The "torch bearer" scans the steppe with a small torch from inside the automobile. On spotting a herd of saiga he switches on a powerful light which blinds the animals and makes them stop or slow down. Shooting is done in the dark from one side at a distance of not more than 30 to 40 m, using buckshot to reduce the possible escape of injured animals, and selectivity is implemented insofar as possible. When the catch is large and the hunt well organised the foregoing is an extremely profitable method.[96] A team can catch 100 or more animals in one night. The hunt is undertaken from August through December, i.e., after the cessation of lactation and before the onset of rut. In normal years roughly 30 to 50% of year-old males and up to 10 to 20% of females of the prior autumn can be shot without harm to the population.

The products obtained from saiga are excellent meat, hide for making chrome leather, and horns. Horns are exported to China where they are used in medicinal tonics. The carcass weight of a male is about 25 kg and of a female 16 to 17 kg. The hide of a male is about 80 dm^2 and of a female 50 to 60 dm^2. In October and November the yield of fat goes up to 8 to 10 kg, on the average 3.0 to 5.0 kg. An average pair of horns weighs about 400 g.

Saiga cause damage to plantations of cereals, perennial grasses, and other crops, and also to forest belts protecting farms. Innumerable instances of damage to green cereals during droughts have been reported. However, the degree of damage is often exaggerated. Even when they run through a field saiga eat only a very small number of plants. For example, in a one kilometer stretch of rye field crossed by saiga only 15 to 20 damaged spikelets were found (Bakeev and Formozov, 1955). Saiga trample more plants than they eat. They visit fields more readily in early summer during droughts. In the Kalmyk steppe significant damage to edible rye and Sudan grass was seen in a few dozen hectares. From among cultivated plants mustard is a particular favorite of saiga (Bakeev and Formozov, 1955). The animals also eat leaves and buds of the seedlings of one-year-old forest belt plants but inflict no significant damage on older plantations (L.G. Dinesman). The insignificant damage caused by saiga to farms is generally compensated many times over by the income from saiga hunting.

According to data collected through questionnaires (A.G. Bannikov and L.S. Lebedeva) the list of plantations damaged by saiga in the Kalmyk Autonomous Soviet Socialist Republic, Rostov district, and Stavropol territory consists of 11 crops cultivated in the steppe region. Information about damage to wheat was contained in 57.1% of all the replies received, maize and millets 47.6%, rye and barley 23.8%, and lucerne [alfalfa] 19.0%. Sudan grass, sorghum, mustard, and melons figured in less than 10.0%. Saiga frequently visited plantations only in droughty years and in the warmest period of the day; evidently they do so mainly to quench their thirst through the intake of succulent plants. Saiga visit plantations of not more than 10 to 25 cm height when the plants are most succulent. Saiga do not visit farms in which the crop is over 80 cm in height. Periods of saiga visitations are not long. In early spring they generally do not visit fields as they are saturated with water at that time and the animals 485 become mired in the soil. Saiga also avoid grown plantations since tall, dense crops render running difficult and also whip the animal's eyes, since saiga run with their head lowered.

---

[96] Nocturnal hunting with a torch by private persons is legally prohibited since it is destructive.

The subject of competition between saiga and sheep in natural pastures has been little studied. However, the coefficient of pasture utilization in Kazakhstan and Kalmykiya by saiga is less than that for sheep. Considering that the intensity of pasture utilization by highly mobile saiga is not much, and that a significant percentage of saiga food plants is not touched by sheep, saiga cannot presently be regarded as serious competitors of domestic animals.

In 1949 saiga were taken to Bulla Island (Caspian Sea along the Azerbaidzhan coast, 40° N lat.) for purposes of acclimatization, but they died in the winter ("Bakinskii rabochii," [Baku newspaper] November 16, 1949). On Barsa-Kel'mes Island (Aral Sea), where only five females remained, eight males were imported in 1929. By 1957 the saiga population there exceeded 1,000 (Sokolov, 1958).

Saiga are easily domesticated. Innumerable instances have been described of young animals living around houses, grazing freely in the steppes, and returning to the house. Fawns five to six days old (those one or two days old often die) are caught for raising in zoological gardens. For the first week they are fed 0.5 liter of milk three times a day.[97] Later, they are put on fresh steppe grass and hay. (A.B.)

Genus of Gorals

Genus *Nemorhaedus* H. Smith, 1827

1827. *Naemorhedus.*[98] H. Smith. Griffith's *Cuvier Animal Kingd.,* vol. 5, p. 352. *Antilope goral* Hardwicke.

1837. *Kemas.* Ogilby. *Proc. Zool. Soc. London,* 1836, p. 138.

---

[97] In the Erevan Zoological Garden saiga calves were once given 150 to 200 g of milk (Gyul'msiryan, 1944).

[98] This spelling is an obvious mistake (*Nemor* or *nemoris* means forest and *haedus* means kid) but some authors use it even now. The spellings *Nemorhedus* and *Nemorrhedus* also occur.

1844. *Caprina.* Wagner. Schreber's *Säugeth. Suppl.*, vol. 4, no. 11, p. 457. Nec d'Orbigny, 1822.

1871. *Urotragus* Gray. *Ann. Mag. Nat. Hist.*, vol. 8, p. 372. *Antilope caudata* Milne-Edwards.

1884. *Nemorhaedus.* Flower and Garson. *Cat. Osteol. Mus. College Surg.*, vol. 2, p. 254. Substitute for *Naemorhedus* H. Smith.

1891. *Cemas.* Blanford. *Fauna Brit. India Mamm.*, p. 516. Nec. *Cemas* Oken 1816 (= *Connochaetes*), nec *Cemas* Gloger, 1841 (=*Rupicapra*). *Nemorhaedus goral* Hardw. (V.H.)

Animals of moderate or slightly smaller size and stout of build. Facial part of skull normally developed; nasals not shortened and nasal opening not enlarged. Anteroparietal region of skull inclined rather gently, while profile of anteronasal region bulges. Preorbital depression on lacrimal and ethmoid pit absent. Nasal broadened in the basal half but do not touch either the premaxillae or the maxillae,[99] i.e., they are in contact only with the frontals and lacrimals, and their lateral margins are free. Lacrimal normal in size; a very small section of its anterior region (at joint with frontal) may reach nasal opening. Main part of bony core of horn elongated, i.e., distance from edge of bony sheath (or its mark on the bony core) to upper edge of orbit greater than vertical diameter of orbit or equal to it. Orbit not tubular.

486 Dental formula:

$$i\,\frac{0}{3},\ c\,\frac{0}{1},\ pm\,\frac{3}{3},\ \ m\,\frac{3}{3} = 32.$$

Horns very short (not more than length of skull), turned back, and form a continuation of line of facial profile, almost straight (only insignificantly turned downward), very sharp, slightly rugose at base, smooth elsewhere, and circular or nearly so in cross section. Keratin black.

Snout normal (not swollen or elongated in form of proboscis); bare section at tip encloses nostrils, covers space between them, and is slightly notched in upper margin. Upper lip hairy apart from a narrow, vertical furrow in middle. Nostrils set forward. Preorbital glands absent,[100] hoof glands present, and inguinal and carpal glands absent. Tail long with a large tassel at end. Ears longish.

Coat fairly uniform in length, usually (at least in winter coat) long and shaggy, and dark. Beard absent. Females only slightly smaller than males with slightly less developed horns. Teats four.

---

[99] Exceptionally, maxilla may touch nasal in a very small section in front of lacrimal.

[100] More precisely, insignificant rudiments are present; seen externally as a section of half-exposed skin.

Inhabitants of rocks and rocky sections in forests from sea level to heights of 2,000 to 2,500 m; goral keep to small groups of 8 to 10 animals.

Goral represent an East Asiatic group distributed (reconstructed range) in upper Burma and Assam; the Himalayas in the west to Kashmir, Kumaon, and northern Punjab, and in the east Tibet and Nepal; southern, central, and northern China (especially Hunan, Szechwan, Fukien, Shensi, Shansi, Jehol, Hupeh, Hopeh, and perhaps other provinces; in Kansu, they are evidently absent), and the eastern part of northeastern China; the Korean Peninsula; and Ussuri and Amur regions (Bureinskiy range). They are absent in 487 Japan. Their range is subdivided in conformity with the disposition of mountains. Goral have vanished at several places in various parts of their range (particularly in Bureinskiy range). The range of the genus is entirely characteristic of the typical Chinese-Himalayan elements of eastern Asia.

Genus *Nemorhaedus* is undoubtedly closest to the genus *Capricornis* (chamois-goat or serow—two species in Southeast Asia and Japan) from which the former differs in rather indistinct craniological features and the absence of preorbital glands. The possibility of the union of these genera into a single one is not excluded. Genus *Nemorhaedus* stands isolated more sharply from other members of the tribe (chamois—*Rupicapra,* and Rocky mountain goat—*Oreamnos*). Together with *Capricornis* goral stand most distant from typical members of tribe Caprini.[101]

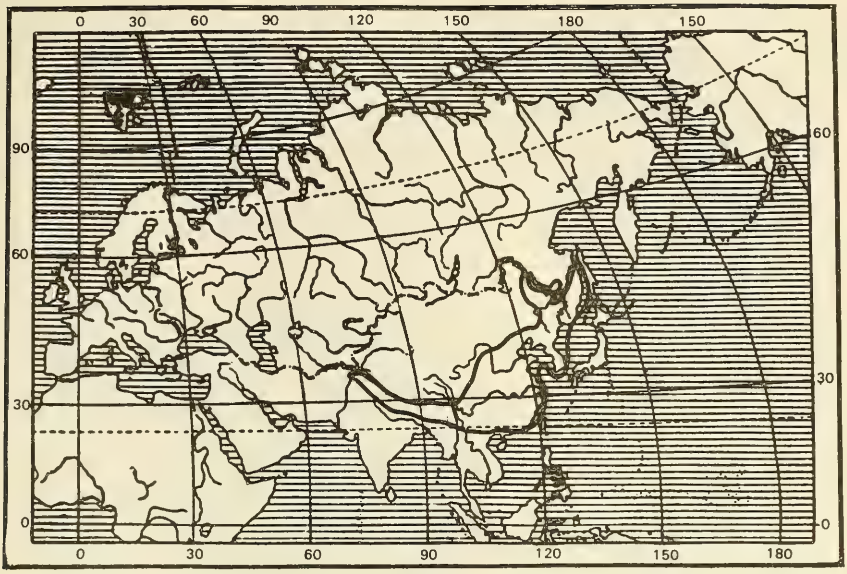
Data on the origin of genus *Nemorhaedus* (and also of *Capricornis*) are absent. They have not been reported in a fossil state. It is possible that the Chinese Middle Pliocene *Pachygazella* belongs to this group. There is every justification for considering the genus as fairly specialized and quite an old form (probably Pliocene) of the southern parts of eastern Asia.

A large number of species have been proposed for the genus. Usually five independent species are recognized (Lydekker, 1913). It has recently been shown that the genus comprises only a single species, *Nemorhaedus goral* Hardwicke, 1825, representing about 4.5% of the species of the subfamily.

Goral are game animals.

---

[101] Sometimes this is emphasized by the fact that *Nemorhaedus* and *Capricornis* are placed in a special tribe, Nemorhaedini, while *Oreamnos* (Rocky mountain goat) and *Rupicapra* (chamois) are attached to Caprini (Sokolov, 1949 and 1953). (V.H.)



486 Fig. 156. Geographic range (reconstructed) of the goral genus *Nemorhaedus* H. Smith. Question marks pertain to territories (Il'khuri-Alin' and Great Khingan mountains) for which information is extremely vague.* V.G. Heptner.

In the USSR only one species of goral[102] is found, representing 0.3% of the species of Russian fauna.

Goral inhabit montane regions in the southern parts of the Far East.

Although a game animal, at present hunting goral is totally prohibited. (V.H.)

14. GORAL

Nemorhaedus goral Hardwicke, 1825

1825. *Antilope goral.* Hardwicke. *Trans. Linn. Soc. London,* vol. 14, p. 518 Nepal, Himalayas.

1867. *Antilope caudata.* Milne-Edwards. *Ann. Sc. Nat. Zool.,* vol. 7, p. 377 Bureinskiy mountains, Amur region.

1862. *Antilope (Caprina) crispa.* Radde. *Reisen im Süden Ost-*

---

*Question marks are absent on the original map—Sci. Ed.

[102] The name "goral" is alien to the Russian language but came into use in the Far East. Moreover this species is called "iman" or "yaman" (from Korean "iman-yan") there. In Manchuria Russians call goral "mountain sheep," "black sheep," or "Amur chamois" (Bromlei, 1956; Baikov, 1915).

Sibiriens, vol. 1, p. 262. Nec Temmink, 1845. Bureinskiy mountains.

1871. *Nemorhaedus griseus.* Milne-Edwards. *Nouv. Arch. Hist. Nat. Paris,* vol. 7, bull. 93. Mupin, Szechwan, China.

1894. *Kemas raddeanus.* Heude. *Mèm Hist. Nat. Emp. Chin.,* vol. 2, p. 240. Amur regions; evidently also Bureinskiy mountains. (V.H.)

Diagnosis

Genus *Nemorhaedus* contains only one species.

Description

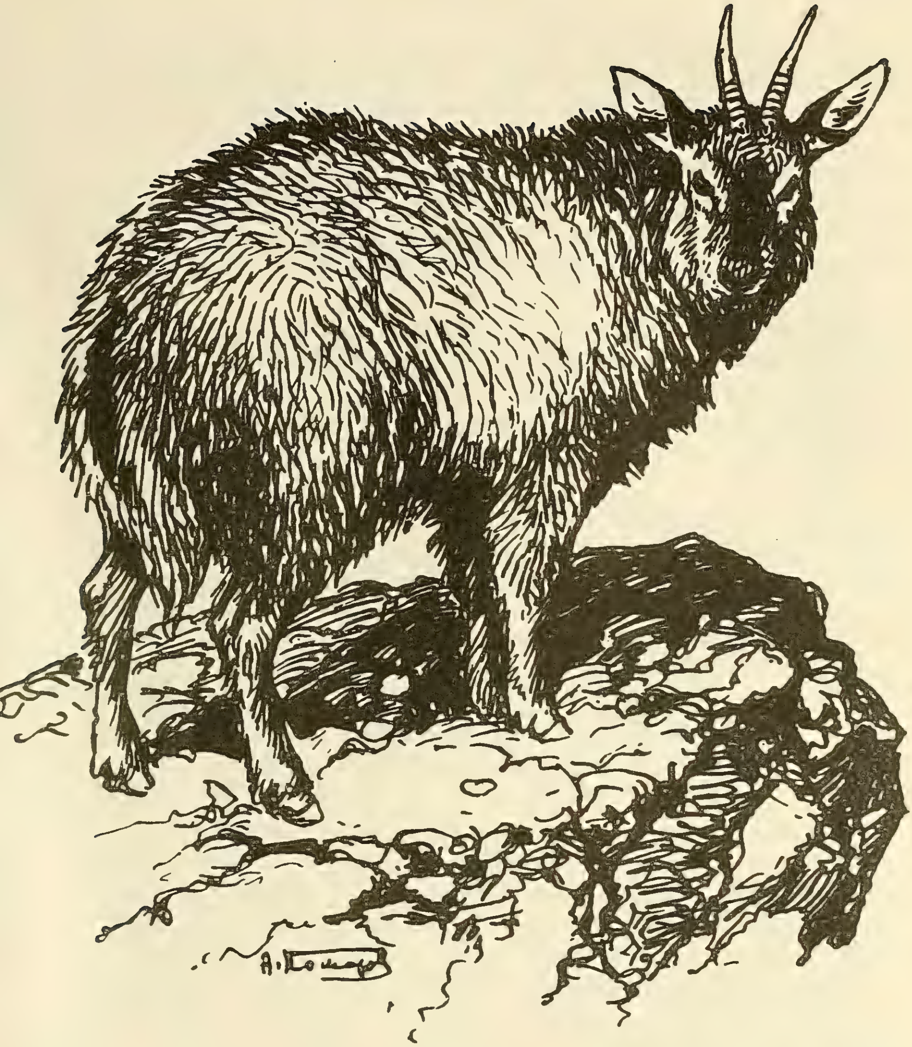
Goral are stout of build, stand on short strong legs, and generally resemble a domestic goat. Chest broad and massive; withers slightly above sacrum. Neck short and muscular. Head small with a swollen profile. Eyes large, dark hazel-colored, with an oval pupil. Ears long. Tail very long with long hair at the end; almost reaches calcaneal joint and imparts a characteristic appearance to the animal.

Horns oily black, more rarely light chestnut in color, set backward, and extend along the line of the profile. They are sharp and only slightly bent down in the form of an arc. Basal half with low transverse ridge. Horns set almost parallel and diverge sideways
489 almost imperceptibly. Only in old males do the distal halves diverge somewhat more sharply, curving slightly to form a faint lyrate figure. Horns smaller and thinner in females than males, and number of rings fewer—17 versus 25 in males.

Hooves have hard borders with a soft "padding" in center portion. Anterior outline circular, which is probably partly due to the wear during movement over rocks.

The winter coat of goral is very long and luxuriant although the hair is coarse and resembles at first sight that of wolf. It consists of about 3.0% guide hair up to 105 mm long, 18% primary guard hair 67 mm long, and 26% intermediate hair up to 45 mm long, and soft, delicate under fur 25 to 30 mm long. The underfur constitutes 53%. On the forehead between the horns and up along the neck to the withers, something like a mane of long (13 cm) bristly hair occurs. A beard is absent but old males have slightly longish hair on the throat, resembling a rudimentary beard. The summer coat is similar but shorter and more sparse.

The color of the winter coat of goral "varies widely even within a given herd. Nevertheless three main color variations are common—



488 Fig. 157. Goral, *Nemorhaedus goral* Hardwicke. Sketch by A.N. Komarov.

gray, rusty-brown, and white. In gray animals, against the general background of ash-gray, a darker stripe with diffused edges is visible from the nose through the head and sacrum to the middle of the tail. Similar dark hair is seen in the posterior part of the forelegs and partly on the chest. White hair covers the upper and lower lips, throat, inguinal region, and caudal base; tassel on tail also white.

"In rusty-brown goral against the ocherous earthy background pale brown or dark ocherous hair is seen at the same place as black hair in gray goral. White hair occurs in the very same regions as in gray goral. Almost white animals or albinos are encountered very rarely. The summer coat of all gorals lacks some of the light-colored fur and appears somewhat darker. Evidently a rusty-brown color is characteristic of old animals and gray of many juveniles. In fact, gorals with gray coats comprise about 61% of the population, rusty-brown 20.7%, and intermediate shades 18.3%'' (Bromlei, 1956). The coloration of animals living on rocks is of protective significance. (V.H.)

The sacs of hoof glands are usually filled with a waxy secretion having a characteristic smell. On the legs and chest of adult goral in winter and summer the fur at places is worn out as a result of climbing on rocks, and sometimes calluses form on the chest and leg joints.

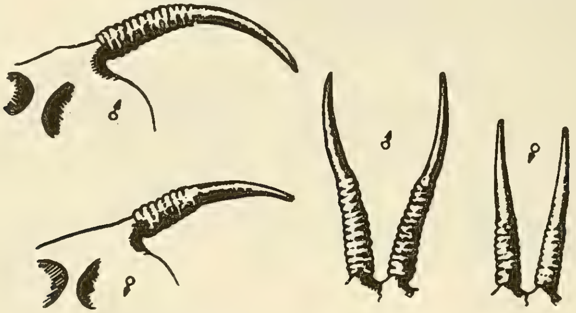


Fig. 158. Goral horns. Sketch by Bromlei, 1956.

Measurements: body length of males (n = 6) 106 to 117 cm[103] and females (n = 3) 106 to 118 cm; height at withers in males 69 to 74 cm[104] and females 71 to 75 cm; chest girth of males 78 to 98 cm and females (n = 2) 70 to 77 cm; ear length of males 13.0 to 14.8 cm and females 14 to 15 cm; length of hind foot of males 28 to 32 cm and females (n = 2) 27 to 30 cm; tail length without hair in males 13 to 18 cm and females 15 to 16 cm; and length of terminal hair on tail of males 20 to 28 cm and females 20 to 27 cm. Horn length of males, measured along the curvature, reaches 212 mm[105] and in females up to 197 mm (Bromlei, 1956). Weight of adult males averages 32 kg and females slightly less. Weight of males can reach 40 kg and even 42 kg, and that of females 35 kg.

---

[103] Possibly up to 123 cm.

[104] Possibly up to 78 cm.

[105] In Manchuria, up to 230 mm (Baikov, 1915).

490 Condylobasal length of skull 213 to 230 mm, and nasals (from lacrimal to distal end) about 55 mm.[106] (V.H.)

Taxonomy

See description of genus.

Geographic Distribution

N. goral is found in the Himalayas, eastern Tibet, montane regions of upper Burma, southeastern and eastern China, Manchuria, the Korean Peninsula, and Amur and Ussuri territories.

Geographic Range in the Soviet Union (Reconstructed)

The reconstructed range in the Soviet Union forms the northern extremity of the range of the species. It occupies an extremely small part of the territory of the Union in the extreme south of the Far East.

Within the Soviet Union the range consists of two parts, which are totally isolated from each other here, but continuous in Manchuria. The western section of the range of goral covers the southwestern part of the Bureinskiy mountains, proceeding toward the Amur valley. The boundary there runs roughly from Pashkov on Amur eastward into the upper Bir (more precisely, to Sutar), and from there, encompassing the upper Bidzhana in the southeast, to the Amur slightly north of 48° N lat. to Pompeevka (Radde, 1862).[107] It is quite possible that in the remote past goral extended northeast and somewhat farther along the Bureinskiy mountains.

The habitat of goral in Bureinskiy mountains is associated with its range in the Little Khingan and comprises its northeastern extremity.

---

[106] Other skull characteristics are given in the description of the genus. The description of goral has been taken mainly from Bromlei (1956 and some unpublished material) and partly from Baikov (1915) and Adlerberg (1932).

[107] At the time of Radde goral were very rare in the Bureinskiy mountains, lived singly, and were widely scattered. Radde's description and map of the range are extremely hypothetical, and his topographic map differs very greatly from contemporary ones. The information given above is a collection from all the data given by Radde and is highly generalized. From among the various occurrences of goral, Radde referred to "the heights at Lagar creek on the left" (the Lagar enters the Amur slightly below Radevka or Radde), along upper Digunsk rivulet entering the Amur slightly above Pompeevka. Moreover, the occurrence of goral has been shown on the right (Chinese) bank of the Amur in the bend at Pashkov. This, according to Radde, is "Dabtal height".

The second section of the range covers Sikhote-Alin and adjoining areas. In the north the range encompasses the uplands on the right shore of the Amur estuary. The mouth of the Amur comprises the northern boundary of the range and the northernmost point of distribution of the species in general. Farther southward the northern boundary runs along the northern edge of the Sikhote-Alin range, but does not reach to the Amur and does not encompass the lower reaches of the rivers entering the Amur from the right (Yai, Khungara, and some others). The ocean forms the eastern boundary; goral are present even on the coastal cliffs. The western boundary is formed by the western slopes of the Sikhote-Alin. The range does not reach the Ussuri valley (Schrenk, 1859). In the south the range extends up to the southern extremity of the Sikhote-Alin and also covers the upland sections to the west and south of Lake Khanka (Maak, 1861) up to the region slightly north of Pos'et Gulf or the so-called Black Mountains (Abramov, 1939), which together with the mountains north of Khanka represent the terminus of the Taipinlin mountainous country in Manchuria.

On the left bank of the Amur, all along the stretch from the estuary to the mouth of the Ussuri and farther west, to the Bureinskiy mountains, goral are absent and were never present.

The range described above shrank over the years. Among the Bureinskiy mountains goral disappeared completely even in the last century and its existence there has been forgotten by the local populace.

491 In Sikhote-Alin the range has shrunk dramatically and its northern boundary described above, based on data for the 1840's and 1850's, has shifted significantly southward. Even by the 1920's goral were absent in the basins of the Kopa and Botcha Rivers (which latter flows into the Tatar Strait at 48°; Emel'yanov, 1927). By 1950 the extreme northern occurrence of goral on the coast was the Naina River mouth (Abramov, 1954), entering [the ocean] slightly south of Cape Amgu,—between it and the mouth of the Kolumba River, i.e., roughly 45°40′ N lat. Deep inside the mountains the habitation of goral is now found in the upper Bikin along the cliffs of its tributary, the Kilou River (Abramov, 1954), roughly at 47° N lat.[108] In the south and southeast the distribution approaches even more closely the very extremity of the range.

Goral likewise disappeared from all the region west of the sources of the Daubikhe and in particular, from the uplands west and

---

[108] The reference that the northern boundary of habitation of goral in the Ussuri region traversed along 45° (Abramov, 1954) thus requires correction.

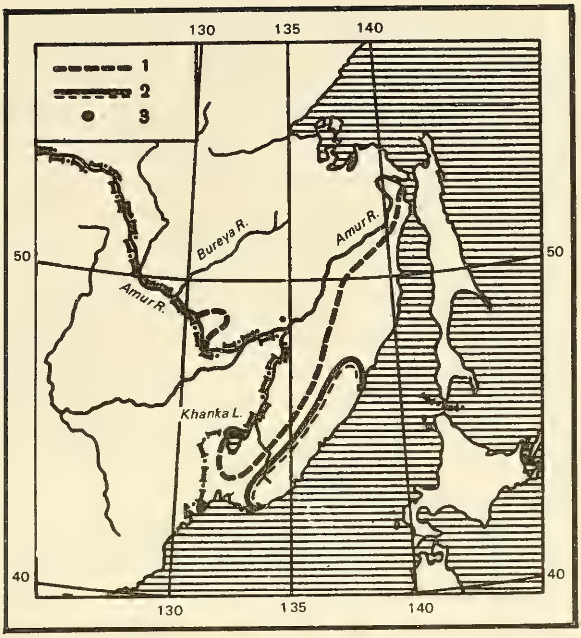


Fig. 159. Boundaries of range of goral, *Nemorhaedus goral raddeanus* Heude, in the USSR.

1—reconstructed boundary, about 1850; 2—boundary of present-day range; 3—habitat north of Pos'et Gulf. V.G. Heptner.

south (southwest) of Lake Khanka. The animal survived there only at one point north of Pos'et Gulf.

Apart from this general southward recession of the range, a significant change in the disposition of the species within it also took place. Formerly, it was quite sporadic but fairly uniform, depending on natural conditions. Goral are encountered now in individual spots, somewhat like colonies, often at very great distances from each other. There are no contacts between such colonies, or contacts are negligible. In Sikhote-Alin at present, in addition to the two northern places of occurrence mentioned above, the following have also been detected: the western slope of the Sikhote-Alin on the Iman River at the villages of Laulyu (slightly, below the mouth of the Armu) and Vakhumbo; the eastern slope at the mouth of the Tetyukhe and farther north to the coastal region of Sikhote-Alin preserve (evidently, this section extends in the north to the mouth of the Naina River). At the southern extremity of Sikhote-Alin goral have been sighted along both eastern and western slopes. They have

been seen on the eastern slope in the region of former Sudzukhin preserve (Sudzukhe River), around Tachin-chtan mountain (the range between the Suchan and Sudzukhe), Tachinchuan and Alekseev, and also in the Pavlina and Three Sisters mountains in the region south of Chuguevka, i.e., on the Sandargou River. Goral have also been seen along Vanchinsk River (Vantsin) and Porusung River (Pkhusun), which enters the sea slightly northeast of the Sudzukhe. On the western slope, goral occur in the upper Tadagou (tributary of the Daubikhe), along the Daubikhe above Vinogradovka and in the Chuguev region in the foothills of Labo-Lazy and Laone-Lazy. In the south goral are found in the region of Suchan on
492 the Malaza River in the vicinity of Molchanovka and Sergeevka villages. In Sikhote-Alin goral are known at a few other points.

Outside this mountain range, in Primor'e, goral still survive in the extreme south on the Sinii Utes massif in the Khasan region north of the Pos'et Gulf (Abramov, 1954).

It is possible that the animals have disappeared at some places in recent years. Evidently they are no longer seen at Iman in the places mentioned above.

Ecological conditions for goral are such (see below) that this species is highly vulnerable to extinction. This was the main reason for its total disappearance from many areas of its range, and for its "spotty" distribution. There is no doubt, however, that natural factors have also played a significant role in changes in its geographic distribution. The Sikhote-Alin represents the extreme northern edge of the range where the species now exists under conditions barely supporting its survival. This is particularly true of the northern half of Sikhote-Alin and the uplands around the Amur estuary. Apparently, however, goral have always been rare there.[109] It is quite natural that all types of unfavorable conditions should come into play particularly sharply there, forcing the range boundary to withdraw southward independent of human influence. With adverse human intervention, the natural multiyear fluctuations (pulsations) of boundaries that are usually associated with climatic cycles, assume a non-recurrent character and become a gradually retreating boundary.

---

[109] Schrenk (1859) reports that goral were fairly common along Sikhote-Alin (which he refers to as "the coastal mountain range—Küstengebirge") south of 50°30'.

Some researchers (for example, Abramov, 1954) have regarded Schrenk's data as suspect. However, the factual information reported by this extremely conscientious and exacting investigator [i.e., Schrenk] about goral distribution is so complete and positive that there is no basis whatsoever for compromising his data, even though they stand in sharp contrast to the contemporary map. Schrenk gives even the local names of the species used by Nivkhis (Gilyaks), Manguns, and Nanaits (Gol'dis).

Geographic Range outside the Soviet Union

The range ouside the Soviet Union includes the Himalayas from the eastern boundaries of Kashmir and Punjab, upper Burma, the eastern extremity of Tibet, southern, central, and northern provinces of China, particularly Yunnan, Szechwan, Fukien, Shensi, Hupeh, Hopeh, and some others (in Kansu, apparently absent), Korean Peninsula, and northeastern China. In the latter goral extend to the Little Khingan, in which region they occur in the Bureinskiy range, hilly segments in the eastern part of northeastern China, extending from the north in the upper reaches of Ussuri and continuing south to the Chan-baishan range, which separates the Korean Peninsula. In this system goral have been sighted on the peaks Chzhanguantsailin, Khengtei-Alin, Lao-e-lin, and Chan-baishan itself. Goral are also found in other places in northeastern China but are evidently absent in the Great Khingan and in Il'khuri-Alin.[110]

The distribution of goral in the above areas is extremely uneven (the range is broken up) and conforms to the disposition of the mountain ranges. The animals have disappeared from many places over a wide area.

Repeated suggestions or conjectures of some past as well as recent researchers (Bobrinskii et al., 1944; Abramov, 1954) about the occurrence of goral in Japan are erroneous. Goral are absent in Japan; only the chamois goat or as it is called, the serai or serow, *Capricornis crispus* Temmink, which are superficially similar to goral, live there. Genus *Capricornis* is very close to genus *Nemorhaedus.*[111] (V.H.)

493 Geographic Variation

The extremely divergent natural conditions in different parts of the range, and in particular its fragmentation (life in the mountains somewhat neutralizes climatic differences) leads one to assume that the geographic variation of the species should be fairly high. Yet no concrete revision of the race structure of the species was done until recently. Only the most obvious synonyms have been eliminated; this covered initially the innumerable synonyms created by Heude. Various independent species of goral have now been united in one. The number of forms acknowledged at present is probably higher than actually exist. Some species have even been separated on the basis of highly variable coloration, which could simply be an expression of dimorphism (Himalayas). Differences between extreme southern (Himalayan) and extreme northern (i.e., Russian) gorals are, however, fairly significant and quite evident. There are also differences in some craniological features (Adlerberg, 1932).

---

[110] Range in Manchuria after Baikov, 1915.

[111] The sources of these errors are original descriptions of Russian gorals (Radde, Schrenk, and some others) in which the name *crispus* Temm. was used (for example, *Antilope crispa* of Schrenk, 1859) pertaining to the Japanese species, and no distinction between the genera *Nemorhaedus* and *Capricornis* made. These investigators clearly showed that what they were describing was a Far East species that lived in Japan and considered this as an important zoogeographic fact. Their error was corrected long ago.

Recently Adlerberg (1932) has again considered the possibility of the occurrence of goral in Japan, but his assumption has not been confirmed nor found acceptance. It was evidently based on unreliable data on one of the specimens examined by him.

In the USSR there is one form.

Amur goral, *N. g. caudatus* Milne-Edwards 1867 (syn. *raddeanus*). The description given above pertains to this form.

Found in the Sikhote-Alin and in the past in the Bureinskiy mountains. Outside the USSR it occurs in northeastern China, Korean Peninsula, Chihli, Jehol, and Shansi.

Some early researchers (Radde, 1862; Schrenk, 1869; Przewalski, 1870; and some others) gave the Russian goral the name *crispa* Temm., 1845, designating it as *Antilope* (*Capricornis*) *crispa* and *Antilope crispa* (see above).

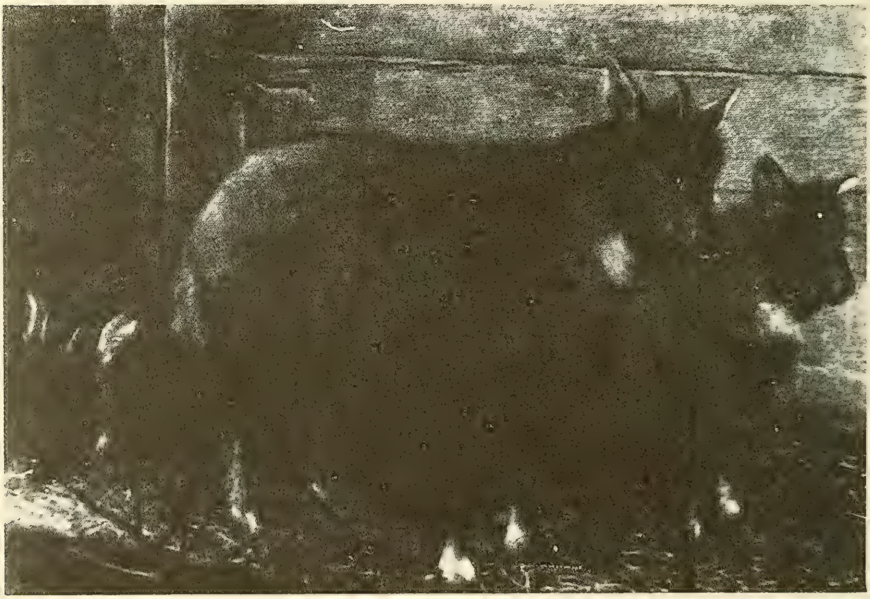


Fig. 160. Gorals in a pen. Sudzukhin preserve. 1937. Photograph by O.V. Vendland.

Outside the Soviet Union usually five subspecies are recognized: *N. g. goral* Hardw., 1825 (Punjab, Kashmir, Kumaon, Nepal), *N. g. hodgsoni* Pok. [Pocock], 1908 (eastern Nepal, Sikkim), *N. g. baleyi* Pok. [*baileyi* Pocock], 1914 (eastern Tibet), *N. g. griseus* M.-E., 1871 (Szechwan, Yunnan, and Burma), and *N. g. arnouxianus* Heude, 1888 (Hupeh, and central China). (V.H.)

Biology

Population. In the Ussuri region goral are distributed in several
494 places. In the last two or three decades fair numbers have been found in the Sudzukhin preserve (Tachin-Chtan range, Tumannaya and Goral mountain, and others) and their population right up to the time of disbanding of the preserve in 1951 remained fairly stable (180 to 220 animals). They were confined there in a territory not exceeding 5,000 hectares (roughly 1/66th of the sanctuary area). Thus the population density was close to 35 to 40 animals per 1,000 hectares. After the closing of the Sudzukhin preserve in 1951 (it was reestablished in 1957), the goral population there decreased notably. In Sikhote-Alin preserve they have always been rare and never numbered more than 30 to 40. The overall goral population in the Soviet Union today (Primor'e region) is presumably 300 to 400 (Bromlei, 1951 and 1956; and others).

Although in 1905 a herd of 30 goral was encountered in the Tachin-Chtan range, herds at present consist of less than 10 animals (Bromlei, 1956).

Habitat. In the Ussuri region goral are found in two types of habitats: coastal precipices and slopes of hills adjoining them, and steep slopes covered with forests in the interior of Sikhote-Alin, on which goral climb up to 500 to 600 or sometimes even 1,000 m (G.F. Bromlei). In the first type of habitat only some stray, poorly developed oak and cedar, shrubby maple, and procumbent juniper are found among the cliffs; there occasionally occur small sections of turf with various grasses. Higher on the slopes grow oak forests. The second habitat, far removed from the sea, abounds in rocky slopes interspersed with small meadows; the forest contains broad-leaved tree species (oak, linden, Manchurian nut, aralia, and others) with an admixture of Korean nut pine (Bromlei, 1956).[112]

The various habitats of goral are often separated from each other by tens of kilometers, in each of which live from a few

---

[112] Here, as at other places, the text of the published works of G.F. Bromlei has been supplemented with his oral and written communications.

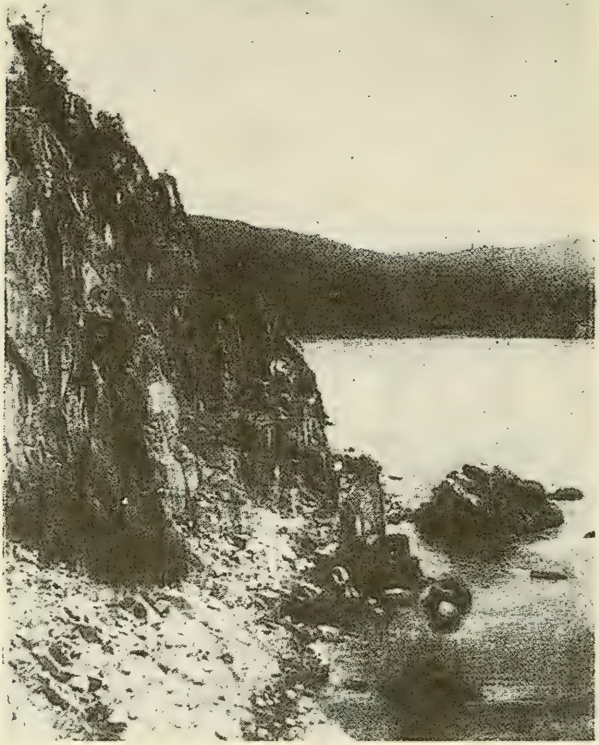


Fig. 161. Habitat of goral in Sudzukhin preserve. Slope of Tumannaya mountain. 1950. Photograph by G.F. Bromlei.

individuals up to 10 or 20 animals.

Food. Utmost diversity in the diet of goral is seen in summer, when over 30 species of plants are consumed (in other seasons, it is slightly over 20, and even less in early spring). In summer goral avidly consume herbaceous vegetation (*Plectranthus,* the grasses: 495 bison grass, meadow grass, fescue, wild rye *Elymus mollis,* as also vetch and others), wild onions, ramson, leaves of linden, lespedeza, wild grape, *Actinidia,* and others; and sedge at the end of summer. Sometimes the animals also consume marine eel grass washed ashore and *Laminaria* seaweed; it is possible that these play the role of mineral nutrients. In autumn, during September, there is a sharp increase in the importance of leaves of trees (up to 80% of vegetative intake, while in summer not more than 20%), which are readily consumed even in dry form. Mostly, these are Mongolian oak and maple, the leaves of which in good weather remain on the branches even in winter. The animals rarely consume withered grass, but the sagebrushes *Artemisia stolonifera* and *A. sacrorum* are consumed in larger quantities than in summer (Bromlei, 1956).

In autumn and winter, when their yield is good, acorns are important but goral can only get at them when the snow cover is not more than 5.0 cm deep, since they do not dig but simply root in the snow with the snout. From autumn to winter the importance of twigs in the diet steadily increases (goral do not touch them in summer); their role is particularly important in February and March when intense snowfalls are quite common in Primor'e territory and acorns and standing dead vegetation become inaccessible. February, March, and early April represent times when food is least available to goral.

In winter twigs of oak and shoots of lespedeza are consumed in maximum quantities and more rarely twigs of ash, linden, wild pepper *Eleutherococcus*, maples, Manchurian nut, and others. Among the trees and shrubs nibbled by goral, the parts consumed first are the thinnest branches and in part buds; bark is gnawed only in the case of severe hunger (more often in March). When food is deficient, the animals also consume arboreal and terrestrial lichens, some mushrooms (wood elm and birch fungi), needles of nut pine, and *Laminaria*. Among herbaceous vegetation, sagebrush, sedge, grasses, and others are important in the winter diet, but on the whole their role is not significant (Bromlei, 1956).

Roughly from early February lanceolate sedge begins to grow on the sunny slopes and is a major food plant of goral until April. In April the snow cover disappears and their diet becomes more diversified. During May feeding on grasses and later on the green leaves of sagebrush, linden, apples, and others, makes it possible for goral to recover quickly (Bromlei, 1956).

Goral visit water holes in summer but depend on snow in winter to quench their thirst.

Home range. Goral are distinguished by attachment to their home range and spend much of the year in an extremely limited area of a few dozen hectares, without moving for grazing more than 2.0 or 3.0 km from cliffs where they find safety from predators. In one case an adult female goral was caught, tagged, and taken 6.0 km from the site of capture; she ran away and soon was spotted in her familiar cliffs. In winter goral are confined to an even smaller area than in summer (G.F. Bromlei).

Daily activity and behavior. No regular rhythms have been recorded in the daily activity of goral; most spend the warm hours of the day in their beds. In the latter half of summer, to protect themselves against blood-sucking flies, some goral go onto the coastal cliffs, returning later to wintering sites.

As a result of their small size and significant weight load on the hoof (365 g per cm^2), goral are compelled in winter to avoid a snow cover of over 25 to 30 cm. If the depth of the snow cover reaches 35 to 40 cm, animals moving on it constantly drag their bellies, rapidly becoming exhausted in snow half-a-meter thick. During intense snowfalls and in the first few days thereafter, goral mobility is greatly reduced and they are exclusively confined to the cliffs until the snow compacts. Many animals suffer intense hunger in this period (G.F. Bromlei).

Vision and hearing are usually considered poorly developed in goral. Goral easily negotiate steep slopes, making swift jumps; the maximum height of a jump is 2.0 m. Callosities usually form on the chest due to friction while jumping among rocks (Bromlei, 1956). Goral are incapable of prolonged running.

496 Goral are confined to small groups; females with their calves live separately in summer.

Seasonal migrations and transgressions. Goral living close to the sea descend to a lower level in winter and congregate on well insolated coastal cliffs where the snow cover usually disappears earliest after a snowfall. In the interior sections of Sikhote-Alin most goral are confined in winter to levels higher than in summer since these parts of the slopes are usually steeper and there is less snow on them. In both regions the spatial magnitude of migrations does not exceed 2.0 km and only in the period of rut do some goral traverse up to 4.0 or sometimes even 12 km, penetrating places they are not found in at other times of the year (Nasimovich, 1955; G.F. Bromlei).

In coastal regions periods of migration into summer habitats and departures from there are determined not so much by the snow cover regime as by temperature conditions and stage of the vegetative period. The growth of vegetation at some distance from the sea in spring, toward May, outstrips that of the coastal section where it is much colder at that time of year; in autumn, however, vegetation ceases earlier at places far away from the sea compared to sites close to it. In accordance with this regime goral in the latter half of April and early May wander farther away from the sea and appear again in October in the region of wintering sites where they remain until spring (Abramov, 1954; and others).

Reproduction. In the goral, rut sets in imperceptibly, without clashes or noisy displays, although males sometimes quarrel among themselves. In the middle or at the end of September adult males and females pair off and separate at the end of October or in November.

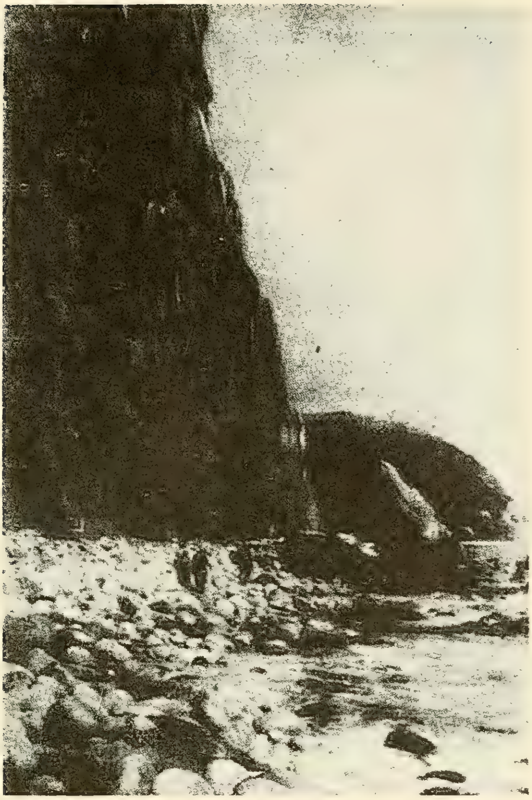


Fig. 162. Abrek village, cliffs of Cape Mosolov. Sikhote-Alin preserve. Site of residence of goral. 1958. Photograph by G.F. Bromlei.

Gestation lasts 250 to 260 days. The majority of females give birth in the first half or middle of June, but some even at the end of May. Calving in July and August is also known. Usually a lone kid, more rarely twins (Baikov, 1915), and rarer still, triplets are born. Parturition usually takes place in the most inaccessible cliff sections under cover of large boulders, which provide the animals protection from heat and heavy showers; a necessary precondition is the proximity of water holes and pastures (Abramov, 1939 and 1954; Bromlei, 1956). Lactation extends into late autumn.

Sexual maturity sets in in the second year of life but only a few animals take part in reproduction at that age (Bromlei, 1956; and others).

Growth, development, and molt. A 10 to 15-day prematurely born offspring weighed about 2.0 kg. In the course of the first month of life the goral kid remains lying down much of the time in a

secluded site; in July it begins to eat grass and tree leaves; by the end of that month it moves rapidly among the cliffs in no way inferior to an adult. At this time young [age two months] weigh about 5.0 kg.
497 In the third month horns are seen which by age one year have reached 115 cm, continuing to grow steadily throughout the animal's life. Kids stay with their mothers up to the following spring and sometimes even longer, up to two years (Abramov, 1954; Bromlei, 1956).

The maximum live weight of adult females is 33 to 34 kg and of males 35 kg or slightly more (Abramov, 1954; Bromlei, 1956).

Molt has not been thoroughly studied in goral. Among animals caught in April winter hair is perceptibly thinned on the back and flanks and gathered in knots, while the flesh is highly pigmented. Remnants of winter wool disappear only by August and a fresh growth of winter wool is again distinctly seen in September.[113] At the end of October the winter coat is fully grown (Bromlei, 1956).

The longevity of goral has not been accurately established; some animals probably survive for 15 years.

Enemies, diseases, parasites, mortality, competitors, and population dynamics. Goral suffer most from wolves, which threaten them not only in the period of rut when goral descend to plains where wolves can rapidly overtake them, but also in winter when heavy snows, ice crusts, and lack of food compel goral to leave cliffs for some time. In the winter of 1940 to 1941 in Sudzukhin preserve some 40 goral died from starvation or wolf attacks. From 1940 through 1947 no less than 26 goral were killed by wolves on Tumannaya mountain. The importance of lynx, leopard, and wolverine is negligible since they are few in number in regions inhabited by goral. Kids are sometimes attacked by yellow-throated marten and probably also by sea eagles (Bromlei, 1956; and others).

The diseases suffered by goral have barely been investigated. Under conditions of zoological gardens goral suffer from paratyphoid. In an autopsy of 20 goral killed at different times endoparasites were detected in small numbers only in two animals (Bromlei, 1956). In goral caught in May in Sudzukhin preserve, and in those that died from June to September of the same year in Moscow Zoological Garden, 26 species of endoparasites were detected including tapeworms, flukes, and roundworms (the intensity of invasion of nematodes reached 637 individuals, of 817 *Ostertagia,* and 142 *Dicrocoelium*). Among helminths in goral there are evidently forms specific to them, for example *Ostertagia nemorhaedi* and *Protostrongylus andrejevi;* the latter is highly pathogenic and may cause severe pulmonary disorders (Shul'ts and Kadenatsii, 1950).

---

[113] Bromlei's (1956) assumption of two molts per year among goral is evidently not correct; summer hair is not shed in autumn.

In spring goral are attacked by ticks; in summer by midges, black flies, and some species of horseflies; and in autumn by red deer bloodsuckers. Hair lice have also been detected in goral (Bromlei, 1956).

In snowy winters goral suffer most from starvation and from wolves. In the winter of 1940 to 1941 and the following spring 14 bodies of goral evidently killed during avalanches were found in Sikhote-Alin mountains at the foot of cliffs (L.G. Kaplanov and G.F. Bromlei). A severe winter is particularly dangerous when autumn is wet and windy, as a result of which most of the dry leaves usually remaining in winter on oak and maple not only blow away but also crumble, thus losing their edible quality (Bromlei, 1956; and others).

The population composition, numbers, and mortality of juveniles among goral have barely been studied. Judging from field counts, females predominate among adults; in various years harems have averaged 1.8 to 2.3 females per male (Bromlei, 1956).

Field characteristics. Superficially the goral is similar to the short-legged goat. The long tail is characteristic (with hair it measures 40 to 45 cm). Males are somewhat larger than females but their coloration is similar; horns of males are larger and more highly curved than in females (Abramov, 1954; Bromlei, 1956).

When frightened, goral emit a hissing sound. The impressions of the front hooves of adult animals quite often reach 4 cm × 6 cm and of hind ones 3.0 cm × 5.5 cm (Bromlei, 1956). The length of jumps on snow ranges between 120 to 140 cm and on hard ground reaches up to 3.0 m. Goral make narrow trails, especially near water holes.
498 In winter the bed occurs directly on snow. Feces are usually in the form of longitudinal pellets 11 to 16 mm × 8.5 to 9.5 mm for adult males and 9.8 to 12.5 mm × 8.5 to 9.0 mm for females. Feces are often deposited at a particular place, one where the growth of herbaceous vegetation is luxuriant (Bromlei, 1956). (A.N.)

Economic Importance

In view of their extremely small population, hunting goral in the Soviet Union has been prohibited. The enlargement of their range by reacclimatization in montane regions of the Far East is desirable.

In the past goral were hunted by shooting, hiding near their trails, drives, or by approaching cliffs in a boat; the animals were caught in nets for zoological gardens (Abramov, 1954). The meat of goral, especially in autumn before the onset of rut, is excellent in quality; its net weight constitutes 55 to 60% of carcass weight, more often 18 to 20 kg. The fur is dense, warm, and beautiful; formerly, it was used in making winter jackets. The top hair is brittle. From the goral carcass, boiled whole (uneviscerated), a jelly used in Tibetan medicine used to be prepared and given to a patient in a dose of one to two ml. Fetuses were similarly used. Udekheits people used the blood (dried) and horns; shavings of the latter were brewed in hot water and used for dressing wounds (G.F. Bromlei). The actual curative properties of these preparations have never been studied.

Most experiments in raising goral in zoological gardens of the USSR have proved unsuccessful as the animals quickly die. (A.N.)

Genus of Chamois

Genus *Rupicapra* Blainville, 1816 (Chamois)

1775. *Rupicapra.* Frisch. *Natur-System d. vierfüse. Thiere,* p. 2. From a nomenclatural viewpoint this name is defective.

1816. *Rupicapra.* Blainville. *Bull. Soc. Philom. Paris,* p. 75. *Capra rupicapra* Linnaeus. Preference is given to Blainville's name in accordance with a resolution of the International Nomenclature Committee (recommendation 91).

1840. *Capella.* Keyserling and Blasius. *Wirbelth. Europas,* vol. 4, p. 28. *Capra rupicapra* Linnaeus.

1841. *Cemas.* Gloger. *Naturgeschichte,* vol. 1, p. 153. *Capra rupicapra* Linnaeus (nec Oken, 1816). (V.H.)

Size moderate and build stout.

Facial part of skull normally developed. Anteroparietal region moderately curved. Skull pneumatization weak. Preorbital depression on lacrimal absent. Ethmoid pit present but usually disappears with age. Nasals of normal structure and size, join frontals, lacrimals, and maxillae. Premaxillae normal in size (not shortened) and their upper processes do not reach nasals. Nasal orifice normal: lacrimal not enlarged and does not restrict nasal orifice. Orbits sharply tubular.

Dental formula:

$$\mathrm{i}\,\frac{0}{3},\ \mathrm{c}\,\frac{0}{1},\ \mathrm{pm}\,\frac{3}{3},\ \ \mathrm{m}\,\frac{3}{3} = 32.$$

Horns small, set vertically, straight for most of their length, and bent with a sharp hook at the end; hook turned back and down.

Horns smooth and circular in cross section.[114] Keratin black. Females also have horns.

Snout normal (not enlarged or elongated in form of a proboscis) with a very small bare patch at the end. Anterofacial profile sharply
501 curved. Nostrils set forward, in form of slits. Preorbital, inguinal, and carpal glands absent; interdigital glands present but relatively small (gazelle type). Pair of special glands found behind horns. Tail short, without a tassel at the end. Ears long.

Pelage uniform in length, but with a patch of highly elongated hair along the sacrum in the winter coat. Beard absent. Pattern of white and dark areas occurs on neck and head. Sharp seasonal dimorphism seen in denseness, length, and coloration of fur. Sexual dimorphism manifested only in some smaller general dimensions and somewhat weaker horns of females. Teats four.

Rupicapra are montane animals associated (in part secondarily) with rocky sections of the alpine zone and upper forest horizons. They occur in small groups.

Their range covers the mountain regions of central and southern Europe, from the Pyrenees to the Balkans and Carpathians, Asia Minor, and the Caucasus, i.e., *Rupicapra* constitute a typical western Palearctic (European) genus. Their range is discontinuous and consists at present of over 15 isolated sections.

Genus *Rupicapra* is highly distinct and in a systematic sense is sharply isolated; a close phyletic relationship with other genera of the subfamily does not exist. Its present and past geographic characteristics are also distinctly those of a typical western form. Genus *Rupicapra* is closest evidently to genus *Oreamnos* (one species—*O. americanus,* occurs in the western part of North America). The latter species characteristically has glands behind the horns. In general, however, *Rupicapra* stands closer to Caprini (tahr, goat, and sheep) than to the rest of the genera of tribe Rupicaprini.[115]

The origin of genus *Rupicapra* is not clear. It is known in the fossil state only from the Pleistocene where the contemporary form has also been found. All paleontological and archaeological finds of *Rupicapra* have been unearthed in Europe (some in the Trans-Caucasus), partly within the present range of the genus and partly outside it, sometimes a fairly significant distance from the present boundaries. In the past chamois occupied the whole of the northern half of the Iberian Peninsula, much of France and Belgium, Germany (roughly up to Berlin in the north), Austria, and Hungary

---

[114] Such a horn design is unique in the family.

[115] For additional comments, see characters of genus *Nemorhaedus.*

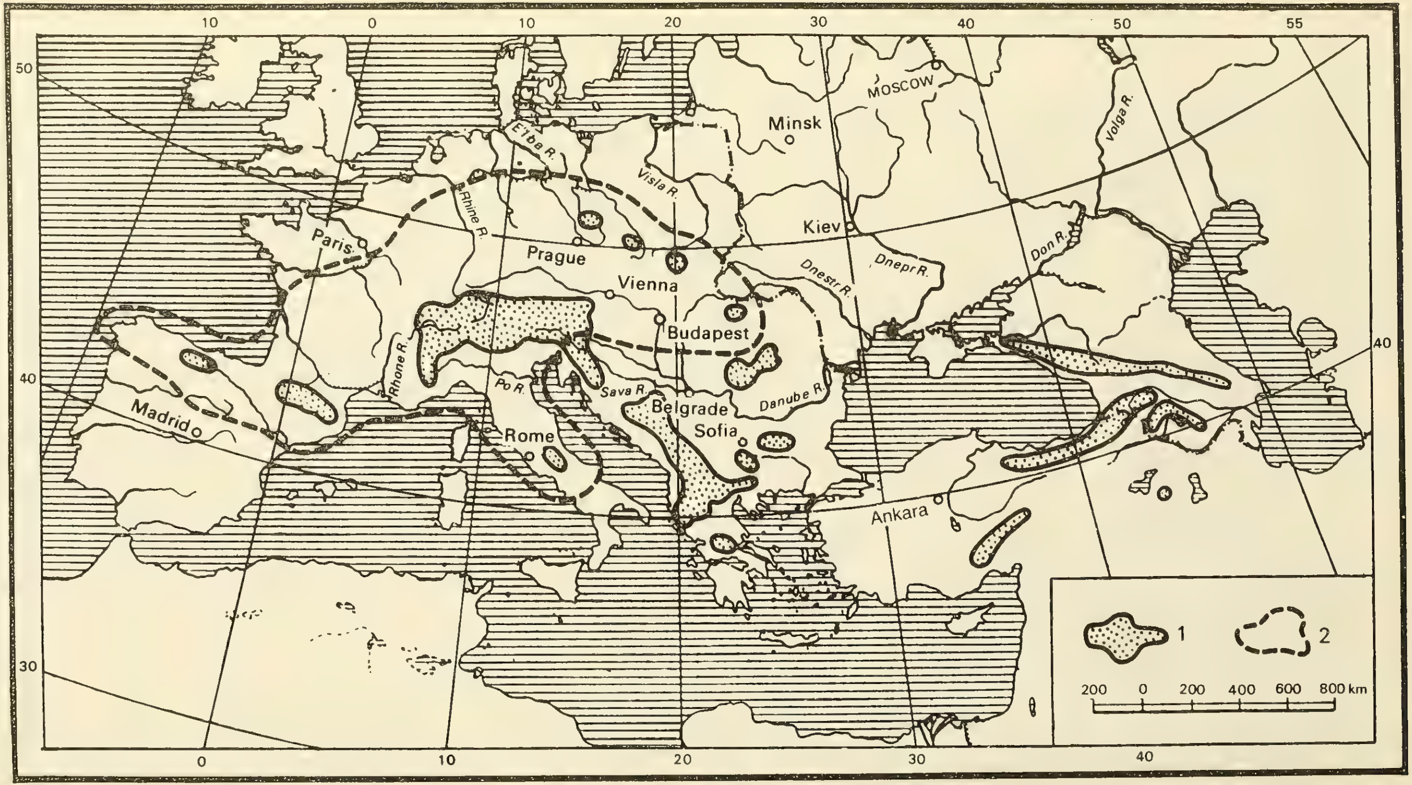

10
0
10
20
30
40
50
55
50
40
30
0
10
20
30
40
MOSCOW
Minsk
Volga R.
E'lba R.
Visla R.
Kiev
Rhine R.
Paris
Prague
Vienna
Dnestr R.
Dnepr R.
Don R.
Budapest
Rhone R.
Madrid
Po R.
Sava R.
Belgrade
Danube R.
Rome
Sofia
Ankara
1
2
200
0
200
400
600
800 km

Fig. 163. Distribution of chamois, genus *Rupicapra* Blainv.

1—Contemporary, or nearly contemporary, regions of distribution in Europe and Asia Minor; also partly reconstructed range in the Caucasus; 2—line limiting distribution of chamois in Europe in the prehistoric period; A—Luzicke mountains and B—Sudety mountains where chamois were acclimatized* (from Heptner, 1936 and Couturier 1938, with modifications). V.G. Heptner.

*Omitted in Russian original—Sci. Ed.

(Couturier, 1938). Thus in the absence of human interference or a minimum amount of it, the chamois was not only more widely distributed in hilly regions than at present, but also survived even at unusually low elevations in western Europe and, what is more, in nearly flat terrain.

Older zoologists recognized many species in the genus. There can be no doubt at present that only one species exists—*Rupicapra rupicapra* Linnaeus, 1758 (about 4.5% of the species in the subfamily).

Only one form of the species is found in the USSR, representing about 0.3% of the species of Russian fauna. This is the Caucasian form, which occupies more elevated parts of the country; in the past it was evidently found in the Carpathians.

R. rupicapra are game animals but hunting is partly prohibited. (V.H.)

15. CHAMOIS, BLACK GOAT[116]

Rupicapra rupicapra **Linnaeus, 1758**

1758. *Capra rupicapra.* Linnaeus. *Syst. Naturae,* 10th ed., vol. 1, p. 68. Switzerland.

1843. *Rupicapra tragus.* Gray. *List Mamm. Brit. Mus.,* p. 167. Renaming of *rupicapra.*

1845. *Rupicapra capella.* Bonaparte. *Atti Sc. Ital. Milano,* vol. 6, p. 377. Renaming of *rupicapra.*

502 1871. *Rupicapra europea.* Cornalia. *Fauna Ital.,* vol. 1, p. 53. Substituted by *rupicapra.*

1897. *Rupicapra dorcas.* Schulze. *Helios. Berlin,* vol. 14, p. 81. Substitute for *rupicapra.*

1908. *Rupicapra tragus asiatica.* Lydekker. *Field,* vol. 112, p. 104. Pontic mountain range near Trebzon, Asia Minor.

1910. *Rupicapra tragus caucasica.* Lydekker Ward's *Rec. Big Game,* 6th ed., p. 338. Caucasus; evidently the northwest in the Laba basin. Fixed as Caucasian preserve.

1938. *Rupicapra rupicapra carpatica.* Couturier. *Le chamois,* p. 369. Retezat mountains, Transylvanian Alps (southern Carpathians), Rumania. (V.H.)

---

[116] The proper Russian name of this form, originating in the Caucasus, is "black goat," which well expresses some features of the general appearance of the animal. "Serna" is of Polish-Ukrainian origin and denotes "roe" (*Capreolus*) which, with some modifications, has been used largely artificially to designate this species.

Diagnosis

Genus *Rupicapra* contains only one species.

Description

The chamois is an extremely slender animal, but less light than goitered or other gazelles and more goat-like in build. Trunk quite massive and short with highly developed chest; neck fairly thin and long, head small, and legs proportional but strong and quite thick.

Head of chamois very constricted on top, ears elongated, narrow, and pointed at tips. Eyes quite large and protruding. Tip of snout covered with hair except for narrow bare patch running from the middle of the upper lip toward the inner corners of nostrils and beyond, surrounding the nostrils. Preorbital glands absent. Occipital glands located just behind horns in the form of two fairly large saccate sheaths with innumerable small glands in their walls.[117] These glands are also present in females and similarly enlarge periodically, but are developed far less than in males and exude no secretion.

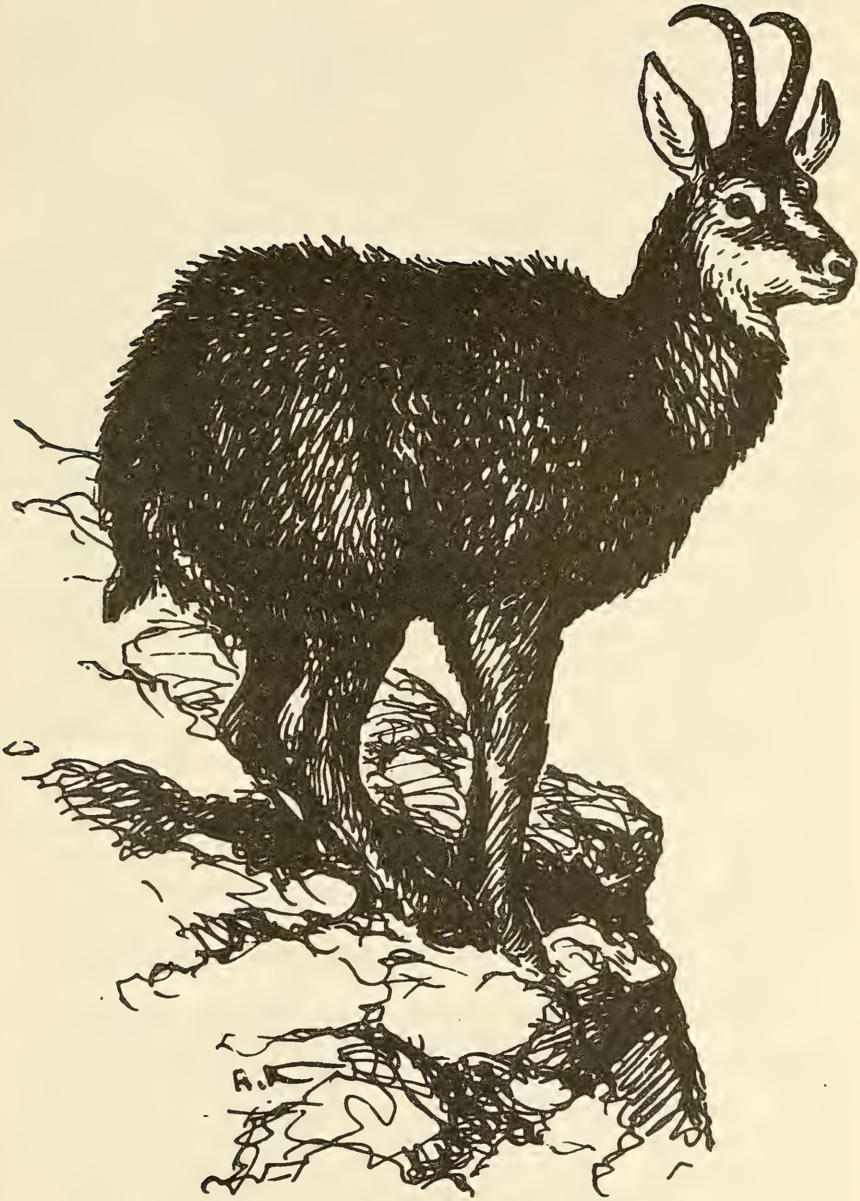
Horns relatively small, thin (circumference of base 7 to 10 cm), and circular in cross section; tips very sharp with an acute backward bend or hook.[118]

Commencing from the base, horns gradually diverge at an extremely acute angle. Distance between their tips usually does not exceed 10 cm. In a few instances horns almost parallel and their tips 4.0 to 5.0 cm apart; they seldom diverge sharply from the base with their tips wide-set and the angle formed by them large. Occasionally, angle between horn bases in proximal half small but becomes quite large midway. Degree of curvature of hooked tips varies little. Horn surface smooth, as though polished, with only indistinct annular wrinkles at the base caused by the growth of annual rings (age of

---

[117] In autumn, when males are in rut, all of this region is intensely swollen and the glands exude a musky secretion with a pungent smell. Males mark their territory at this time with this secretion.

[118] The horn structure of chamois creates difficulties and sometimes confusion when attempting to assess its biological significance. Often its importance is questioned or even totally ignored. In any case, the assumption that falcate horn tips may play, as in goats, the role of a hook while negotiating rocky mountains or of a brake while descending extremely steep slopes (Sokolov, 1953, p. 158) begs credulity and is unacceptable. Without embarking on a discussion of this subject, one cannot refrain from mentioning that they certainly look menacing when a chamois assumes an aggressive pose (head dropped low). Their unusual and abruptly vertical disposition on the skull largely balances the falcate flexure of the tips.



500 Fig. 164. Chamois, *Rupicapra rupicapra* Linnaeus. Drawing by A.N. Komarov.

chamois can be accurately ascertained from the number of rings). At the very tip faint longitudinal wrinkles are also visible. Keratin deep black. Horns of females only slightly thinner and smaller than those of males.

Given the size of the animal, its hooves are fairly large and strong but narrow, with an extremely pointed anterior margin. The midportion of the hoof is fairly soft but its rim is hard and sharp, especially the posterior margin. This makes it possible for these
503 mountain animals to move on hard ground and steep inclines and to grip even insignificant projections. The lateral hooves of the fore- and hind limbs are well developed, about 2.5 cm long and almost 4.0 cm wide. They act as effective braking devices while descending (gliding down) sheer slopes. Tail very short and much of its lower surface bare.

Overall coloration of summer coat rusty-red, sometimes reddish-chestnut. From the occiput to the caudal base runs a narrow (not more than 3.0 or 4.0 cm wide) stripe of lustrous blackish-brown or black hair. In some animals this stripe is not seen on the neck, or the sacrum anterior to the tail. The middle of the back is more vivid in color while the sides become lighter. From the axillary region (from the elbow) up to the groins along the underside of the flanks at the abdominal boundary, a broad blackish-brown or grayish-brown band occurs. It gradually merges upward with the color of the flanks but is sharply demarcated below from the light rusty-yellow or yellow color of the abdomen. Wool of the groins is whitish. Front of chest covered with dark brown pelage. Color along the neck same as that of back or slightly darker. Thighs rusty-red, being lighter on the rear than elsewhere on the body, i.e., whitish with a rusty tinge or sometimes almost white. From the hock down the color of the posterior surface of the legs is grayish-brown. Anterior surface of hind legs from the knee dark brown or blackish-brown. Forelegs from elbow joint almost to hooves blackish-brown, almost black in some cases. At the hooves there are usually areas of a chestnut color. Tail at its base chestnut with elongated reddish-brown or blackish-brown hair at the tip.

Head, compared to trunk, much lighter, of a fairly bright yellow, sometimes whitish color. Lower jaw and throat of same color. Inner surface of ears dirty white or white and outer covered with grayish-brown hair; tips of ears blackish-brown. From the base of the ear, through the eyes, toward the corner of mouth, sometimes also toward the corner of the nostrils, there occurs a dark brown band about 2.0 to 3.0 cm in width. Size of this band, its outlines, vividness, and in general the entire facial pattern varies greatly. Sometimes, for example, a dark band commences from the base of the horns and runs toward the eye and from the latter to the upper lip; often, a dark-colored short area extends forward from the base of each horn; sometimes the whole region of the horn base is dark brown, and so on. In some individuals the light color extends not only to the throat but also to the upper portion of the neck.

Hair throughout the body dense, bristly, for the most part wavy, and up to 3.0 cm long, but shorter on head and legs.

Winter coat consists of long guard hair up to 12 cm long, and dense underfur. On withers and back a crest of particularly long hair occurs, attaining a length of 15 to 17 or even 20 cm.[119] General color of the animal in full winter coat dark brown, mane on withers and back black or almost so, and hair tips often lighter (whitish). Bands on head blackish-brown, and occiput, upper part of neck, and throat light-red or yellowish-red. Scapular region almost black, ventral part of chest light brown, and posterior part of thighs bright chestnut. Individual color variations in the winter coat, as in the summer, are quite distinct.[120]

There are no sex-related color differences. The color of the young is chestnut and more uniform than in adults, but with a dark line along the back; facial pattern the same as in adults.[121]

The size and weight of chamois reflect considerable geographic variability. On the average the species is characterized by a body length of 125 to 135 cm, height at shoulders 70 to 80 cm, length of ears about 12 cm, and length of tail 5.0 to 8.0 cm. Males weigh 30 to
504 50 kg and females 25 to 42 kg. The largest animals weigh 56 kg or even exceed 60 kg. Total skull length reaches up to 22 cm, and maximum horn length up to 31 or even 34 cm (Couturier, 1938), but usually much less.[122] Females somewhat smaller and lighter than males, with shorter and thinner horns. (V.H.)

Taxonomy

See the description of the genus.

---

[119] From these hairs are made the chamois "beard" highly prized by western hunters, consisting of hair tied in a special manner, attached to a hunter's hat.

[120] The coloration described is that of Caucasian chamois and mainly from Dinnik (1910) with additions.

It is generally thought that chamois undergo only one molt, in spring, and that the winter coat reflects the growth of guard hair and under fur. Quite recently, however, it has been shown that a true autumn molt also occurs.

[121] Skull characteristics are given in the description of the genus.

[122] More data on Caucasian chamois are given in the section on Geographic Variation.

Geographic Distribution

This species is encountered in the mountains of southern and south-central Europe, Asia Minor, and the Caucasus.

Geographic Range in the Soviet Union

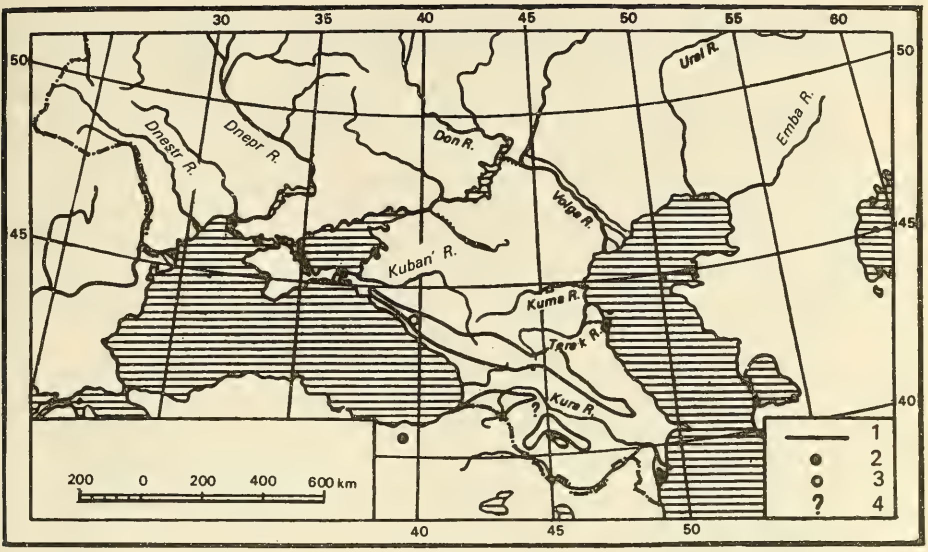
The range in the Soviet Union (reconstructed) covers the Great Caucasus range and the mountains of the Little Caucasus, and possibly also the extreme southwestern part of the Carpathians bordering Rumania.

The range of chamois in the Caucasus was evidently not continuous over the historic period. Part of it covered the Great Caucasus range and another, the Little Caucasus. It is also evident that the latter was subdivided into some isolated pockets as a result of the subdivision of the Trans-Caucasus into separate, more or less isolated mountains.

Chamois nowadays inhabit high mountains. This, however, is mainly the result of their displacement by man. In general these animals do not avoid lowlands, not even at very low levels, and can survive almost on the plains. This was indeed the case in the prehistoric period in Europe (see below). Isolated regions of chamois habitation may thus be regarded as originally continuous. This was probably also the case in the Caucasus. There is no doubt, however, that in the historic period the region of chamois habitation in the Great Caucasus stood isolated from the Trans-Caucasus. No material is available at present to reconstruct the geographic range
505 obtaining in the historic period in the Trans-Caucasus. In the Great Caucasus it probably not only extended from the western to the eastern extremity, but evidently reached almost to the plains on both slopes.

The former range of chamois in the Caucasus, for which a conception, primarily for the nineteenth century is possible, has changed markedly now in the direction of reduction. This process was particularly intense at the end of the nineteenth century and in the first few decades of the present century.

Reduction of the range proceeded and continues to do so in two directions—shrinkage from the periphery and withdrawal into high mountain regions. Thus in the western Caucasus even at the end of the nineteenth century chamois were encountered in the zone of Chernye mountain, i.e., along the first of the level strata of the Great Caucasian range, and in the south along rocky sections not far from the sea (Nasimovich, 1949). This process has occurred all along the periphery of the range.



504 Fig. 165. Geographic range of chamois, *Rupicapra rupicapra caucasica* Lyd., in the Caucasus, reconstructed for the middle to the end of the nineteenth century (highly schematic; scale in km).

1—western limits of distribution in the Great Caucasus range; 2—type locality of *R. r. asiatica* Lyd. in the Pontic range in Turkey; 3—extreme western point of contemporary distribution of chamois; 4—region of possible link of both geographic ranges in the past. At present the animal is not found in the Little Caucasus. V.G. Heptner.

On the other hand, in regions where chamois were distributed uniformly and densely (as is common under montane conditions), their range is now broken into isolated pockets separated from each other by significant stretches in which the animal is not found. Populations on these "islands" are low and survive practically in isolation from the main population.

The foregoing processes are simultaneous, and withdrawal of the general boundaries often proceeds through the stage of formation of isolated pockets. In a significant, evidently large, part of their range chamois currently survive in small isolated pockets. This situation obtains in the central and eastern parts of the Great Caucasus. On the whole wherever the animals still survive their range has retreated into high mountains.

Chamois have disappeared altogether in some mountain ranges. This is particularly true of Little Caucasus (see below).

At the end of the last and in the first few decades of the present century, the chamois range in the Great Caucasus at its western extremity commenced at the upper reaches of the Pshada River and

Goitkh Pass (the road to Tuapse runs here), roughly 60 km from the northwestern end of the range at Anapa,[123] and extended up to its eastern end. The extreme points of occurrence of chamois there are the massifs of Shakh-Dag, Shalbuz-Dag, and Bazar-Dyuzi in eastern Dagestan and Babadag mountain (south of the main axis) within Azerbaidzhan. The range was associated with the highest parts of the mountain range and was in the form of a generally narrow strip, the width of which varied considerably. The region of chamois distribution was widest and most continuous in the western Caucasus. There the animal was seen even at extremely low levels, reaching into the Kuban basin in the north up to Psebai, and on the southern slope not far from the sea above Adler, Sochi, and farther west. The distribution of chamois was less extensive in the central Caucasus and in the ranges to the east. There in some respects the natural conditions for existence were probably less favorable, and the human population in this part of the mountains being denser, persecution was also greater.

In Trans-Caucasus there were some individual sections of the range in the Murov-Dag, Shakh-Dag, Pambak, and Papakar ranges located to the east, north, west and northeast of Lake Sevan and the Aragats massif.

Other areas of distribution of chamois were the Trialets and Adzharo-Imeretin ranges (particularly the regions of Borzhomi and Beloe Spring, close to Batumi, and other places). In the recent past these were evidently isolated areas of occurrence separated from those farther east. However, it is highly probable that the entire area was continuous in the remote past.

506 In the period under description, and probably even before, chamois evidently were not present in Karabakh and Zangezur and other mountains, and were evidently absent right from the beginning, or in any case in the period under description, in Talysh range.[124]

At present the range of chamois is dramatically smaller. In Armenia and adjoining places in Georgia (the abovementioned ranges run toward Sevan and Aragats) they have disappeared altogether.[125] Evidently this is true of other Trans-Caucasian habitations of chamois listed above (information not available in literature).

---

[123] "Quite often . . . , in winter, these animals were killed even at 15 to 20 versts southeast of Novorossiisk, in the hills not far from Kabardinka village; but the animals were driven there probably under some exceptional conditions of deep snow in the higher region . . ." "Commencing, however, from Goitkh Pass eastward, chamois were encountered everywhere in the Kuban region" (Dinnik, 1910).

[124] Information about chamois distribution in the Trans-Caucasus in the period under description, as can be judged even from the work of Dinnik (1910), is extremely scanty. It is possible that the animal was dispersed far more widely than is imagined today. In the Trans-Caucasus chamois at places, for example the northern slope of the Shakh-Dag range (Shamkhor and Akstafa basins), also descended very low.

In the Great Caucasus range the geographic range has generally preserved its former overall features although significantly contracted. The largest section of chamois habitation was formerly in the western (Kuban) Caucasus and was associated with the Caucasian preserve. The western point of habitation lies on the main axis of the mountain range, roughly at its intersection with 39°30′ E lat. on the Pshekha River west of Fisht and Oshten. The farthest limit of occurrence in the east has evidently not changed.

Both the northern and southern limits of the range receded at most places into the high mountains and the area thus narrowed. This reduction was least in Caucasian preserve and places adjoining it. There chamois evidently still occupy not only the highest parts in the central Great Caucasus range, but also those lying north of it, i.e., the Skalistyi [Rocky] mountains and probably even sections of the peripheral range—Chernyi [Black] mountain (Psebai). On the southern slope in this part of the region the range boundary at places falls just 10 to 15 km in a straight line from the sea coast (Sochi; data for the 1930's).

In general, from the preserve to the upper reaches of the Terek, chamois are evidently present on both sides of the mountain range, but farther eastward mostly along its southern slope. This strip, apart from the extreme western portion, is generally very narrow, at places highly narrowed, and at many places interrupted. Thus, in the Teberdin basin chamois are absent or negligible. They are evidently absent in southern Ossetia, sporadic in northern Ossetia, but are absent all along the Georgian Military Highway and in the Kazbek massif. They are absent almost throughout Dagestan apart from the above-named massifs, and so on. Evidently, the range of this species in the Great Caucasus could more appropriately be regarded as a chain of isolated sections. However, details of distribution of chamois in the Caucasus are not known.[126]

Chamois in the past were evidently encountered in the Russian part of the Carpathians and in the extreme southeast in the region adjoining Rumania. Places for its habitation are favorable there

---

[125] In the latest lists of fauna of Armenia (Dal', 1954) chamois are not even mentioned.

[126] The range of chamois in the Caucasus is based on data of Nasimovich, 1949; Vereshchagin, 1947; Heptner and Formozov, 1941; Dinnik, 1910; and some others; and also on original material of V.G. Heptner.

(Pop-Ivan, for example) and chamois are present in the Rumanian territory immediately adjoining the Soviet Union.

Geographic Range outside the Soviet Union

At present the range covers the Pyrenees and the Cantabrian mountains, the Alps including the Savoy, Maritime, and mountain regions north of Grenoble (Chartres [sic], France), Apennines (now only Abruzzi), Tatra and Transylvanian Alps (southern and eastern Carpathians), mountains in the western half of Yugoslavia and eastern Albania, mountains of Greece in the south up to the Gulf of Patrai, the Balkan ranges (Stara Planina), Rodopi, mountains of Asia Minor (Pontic range, Kilikii Taurus, Antitaurus, and Armenian Taurus), and the area southeast of Lake Van. It is quite possible that chamois have now disappeared from some of these places.[127]

The range of chamois is thus divided into over 15 sections. This discontinuity is largely the result of human activity. There is no doubt that in the prehistoric period chamois spread through low mountains or even plains, and isolation of the more important 507 pockets of habitation was not so total. Archaeological, and certain paleontological material, demonstrate that chamois in the present-day form, even in the Paleolithic and Neolithic periods, were distributed throughout the northern half of the Iberian Peninsula, almost the whole of France (apart from the northwestern portion), southern Belgium, much of Germany (north roughly to the latitude of Berlin), Czechoslovakia, Hungary, northwestern Rumania, and southern Poland (Fig. 163). Instances of transgression of chamois from the Alps into the Schwarzwald are presently quite significant. (V.H.)

Geographic Variation

Geographic variation in chamois is quite extensive, i.e., evidenced in a significant number of forms, but the magnitude of this variability or sharpness of differences, is not great. While all the forms are quite close to each other, some are extremely close. This indirectly confirms the relatively incomplete isolation of the different populations and areas of occurrence in the past. It is possible that the actual number of geographic forms is somewhat less than now assumed.[128]

---

[127] In the Sudeten and Luzicke mountains (Czechoslovakia) chamois have been acclimatized. The range outside the Soviet Union has been taken from Couturier (1938) but supplemented from other sources.

[128] A more complete analysis of geographic variability of chamois has been given in the monograph by Couturier (1938).

In the Soviet Union one, or perhaps two forms occur.

1. Caucasian chamois, *R. r. caucasica* Lydekker, 1910.

The description given above is that of the Caucasian chamois. Measurements[129]: height at shoulders 78 to 86 cm, height at sacrum 84 to 94 cm, length of ears 12 to 14 cm, and weight of adult males 32 to 36 kg, reaching in rare cases up to 40 kg. Overall length of skull 20.7 to 21.3 cm, height of horns in males 21.8 to 26.0 and in females 15.2 to 20.6 cm.

This form is found in the Caucasus. It does not occur outside the Soviet Union.

The taxonomy of the Caucasian chamois has not been studied thoroughly and available information is contradictory. Thus, according to Dinnik (1910) it is larger than the Alpine form and characterized by light field on the head of much brighter chestnut color. According to Couturier (1938), whose views are based on a large sample of material, the Caucasian form is of somewhat smaller dimensions than the Alpine. It may be taken as established that the horns of the Caucasian chamois are shorter and weaker than those of the Alpine form. In general, however, it has now come to be recognized that this is a barely distinguishable form and close to the Alpine form (Couturier, 1938).

The relation of the Caucasian form to *asiatica* Lyd., described from the northeastern part of Asia Minor (Pontic range in the Trabzon region), requires a special study. Information on differences between these forms available in literature is highly incomplete. Evidently they are extremely proximate and the assertion (Couturier, 1938) that *R. r. asiatica* Lyd. differs more from the Alpine form than from *R. r. caucasica* Lyd. is dubious. It is highly probable that the Caucasian form is identical to *R. r. asiatica*. This is particularly true of the Trans-Caucasian population, the range of which directly merges with that of *R. r. asiatica* in the Pontic range via the Adzharo-Imeretin mountains (chamois are known even around Artvin). How close the relations between the Great Caucasus chamois and *asiatica* are, is difficult to say since a comparative study of the Great Caucasus and the Trans-Caucasus forms has not been done to date. It is highly possible that the form *caucasica* exists but is restricted to the Great Caucasus range, while *R. r. asiatica* exists in Trans-Caucasus, at least in its western part. Due to the complete destruction of the Trans-Caucasian chamois, its systematics cannot now be resolved.[130]

---

[129] There is almost no information about the size of Caucasian chamois and a fairly accurate description of the Russian chamois has remained impossible so far. The measurements cited above are from Dinnik (1910; body) and Couturier (1938; skull and horns). The measurements of body length given by Dinnik are inaccurate and hence not given here. The average horn length of the Caucasian chamois, measured along the curvature, is 20 to 22 cm, sometimes 23 cm, and rarely 24 cm according to Dinnik (1910).

508 2. Carpathian chamois, *R. r. carpatica* Couturier, 1938.

Overall length of skull 22 cm, length of horns up to 30 cm, and weight 50 to 60 kg.

This form was formerly sighted in the extreme southwestern part of the Carpathians adjoining Rumania. At present it is extinct. Outside the Soviet Union it occurs in the Transylvanian Alps and Carpathians within Rumania.

This is evidently a very distinct form, differing from all others in its large size.

Apart from the above races, according to a recent revision (Couturier, 1938), seven more forms[131] are recognized outside the USSR: *R. r. rupicapra* Linn., 1758 (Alps), *R. r. cartusiana* Cout., 1938 (Chartres [sic] region north of Grenoble in France), *R. r. balcanica* Bolkay, 1925 (Balkans), *R. r. asiatica* Lyd., 1908 (Asia Minor), *R. r. ornata* Neum., 1899 (Italy and Arbuzzi), *R. r. pyrenaica* Bonap., 1845 (Pyrenees), and *R. r. parva* Cabr., 1911 (Cantabrian mountains, Spain). Among these, the most distinctly characteristic ones are evidently the Alpine and Pyrenean forms. (V.H.)

Biology

Population. At present the chamois is found in the Caucasus mostly in preserves. In Caucasian preserve where these animals are generally counted annually, their population in 1936 and 1937 when the territory of the preserve was 300,000 hectares was estimated at a minimum of 4,000 (Nasimovich, 1941). In 1939 over 3,200 chamois were counted and their total population estimated at 12,000 (Zharkov, 1940). In Lagodekh (13,000 hectares) and Zakatal' (29,000 hectares) preserves,[132] respectively 600 to 1,000 chamois were counted (Enukidze, 1953; I.F. Popkova). In Teberdin preserve (70,000 hectares) 20 to 40 chamois were sighted per 1,000 hectares of area suitable for them[133] (Z.S. Ekvtimishvili), and the total population according to the 1955 count was roughly 1,000 (Inyakova, 1957). Among other regions, those particularly abundant in chamois are some montane regions of the western Caucasus and a part of Georgia (in particular Abkhazia). In much of the remaining geographic range in the Caucasus chamois are relatively few, this being particularly true of the Little Caucasus, Kabardino-Balkaria, Northern Ossetia, Dagestan, and Azerbaidzhan. In all these regions reserves of chamois have notably diminished.

---

[130] From the Pontic range two forms of rodents penetrate into the western Trans-Caucasus, USSR: these are the red-backed mouse (*Clethrionomys glareolus*) and wood mouse (*Apodemus mystacinus*). Such an event is even more probable in the case of chamois.

[131] Couturier (1938, p. 386) listed eight forms but the inclusion of one of them (*olympica*) is clearly erroneous (see p. 346 [in Couturier]).

[132] In all cases the area inhabited by chamois is much smaller.

[133] Actually, this is per 1,000 hectares of area.

The distribution of chamois 50 to 80 years ago in the Caucasus was markedly more extensive and its population far greater. Even in the upper reaches of the Beloe and Laba where chamois even today are abundant, their population was still higher in the 1870's to the 1890's and instances of encountering chamois in groups of 100 animals were not rare. Radde (1899) found groups of some hundreds of chamois in the Trans-Caucasus. At present in Caucasian preserve encounters of herds numbering over 100 animals are exceptionally rare. In Zakatal' preserve from 1953 to 1957 no more than 40 animals occurred in a single herd (I.F. Popkova); in the first few decades of the twentieth century there, and also in the present Lagodekh preserve, chamois herds of 100 to 200 animals were sighted (Markov, 1938).

Habitat. Caucasian chamois inhabit regions with an extremely humid climate and heavy precipitation in the form of snow (western Caucasus) and also relatively dry and low-snow regions (Dagestan, Armenia, and others). The vertical range of distribution is extremely variable, from 400 to 3,500 (northwestern Caucasus), reaching even 4,000 m (Trans-Caucasus).[134] At the end of the last century small groups of chamois were sighted in winter close to Khosta and Gelendzhik at heights of 150 to 200 m above sea level.

In the western Caucasus chamois may occur in summer in a broad mountain belt but they are particularly abundant at this time
509 of year at heights of 1,700 to 2,500 m among alpine and subalpine meadows and in the upper one-third of the forest belt. Chamois are confined to very steep and rocky slopes but sometimes emerge to feed in open alpine pastures with relatively gentle slopes, such as small montane plateaus and the bottoms of broad glacial troughs, and at other places where they are least threatened by man. Tur [*Capra*] are encountered extremely rarely in such localities. Chamois avoid overgrown dense gorges into which tur often descend on summer days. Thus, the habitats of chamois and tur do not usually coincide. Cha-

---

[134] The maximum height at which tracks of alpine chamois were seen at any time was 4,750 m on Mt. Blanc (Couturier, 1938).

mois are usually confined in summer to the extremely high alpine belt of the Dagestan mountains, where they occur even above bezoar goats [*Capra aegagrus*] and tur (Heptner and Formozov, 1941). This is largely due to the high level of permanent snow in Dagestan. In many regions of the Caucasus, especially at places where the animals were intensely persecuted by hunters in the past and in alpine pastures easily accessible to man, the majority of chamois spend the entire year in the forest belt at heights of 700 to 2,000 m above sea level (Ossetia, Alazan River basin, and others).

In Zakatal' preserve chamois are often seen in the daytime among subalpine tall grasses (I.F. Popkova); in Caucasian preserve chamois avoid such localities.

Chamois summering in alpine meadows usually descend into the forest in winter.

Food. In Caucasian preserve chamois consume over a hundred species of plants. In summer forbs are consumed maximally; sedges, legumes, and grasses are of less importance. In May in mountain pastures the sessile leaves of herbaceous vegetation are the first to be nibbled (especially plantain *Plantago saxatilis,* anemones, and lady's mantle); in June young shoots and leaves and blooming racemes are also consumed (apart from those stated above, chamois avidly consume pasque flower *Pulsatilla,* caraway *Carum caucasi-*

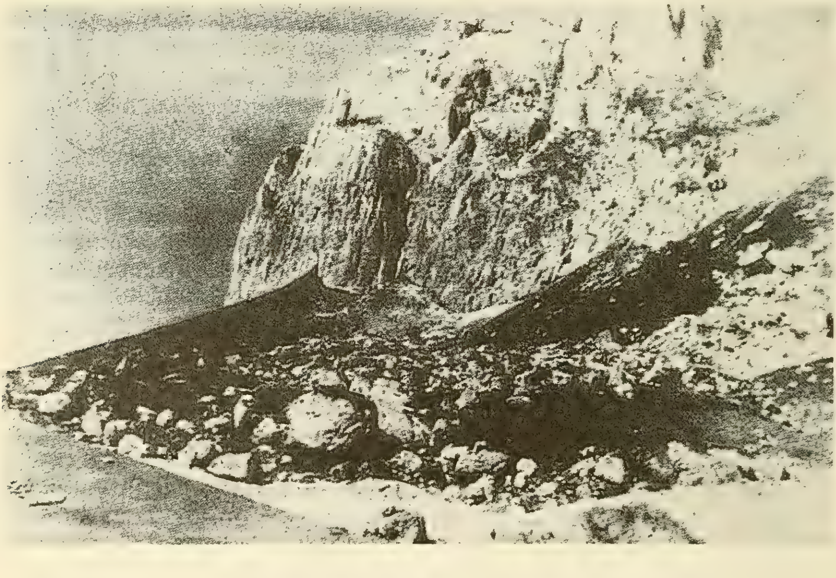


Fig. 166. Habitat of chamois in the western Caucasus. Oshten Mountain. July, 1949. Photograph by I.V. Zharkov.

cum, chervil *Chaerophyllum aureum, Inula, Pedicularis,* and others). In July the diet consists predominantly of racemes and buds (*Rumex acetosa, Aguilegia, Pedicularis,* valerian, Compositae, bluebell, and others) and in August racemes and fruits (especially of Compositae). In September chamois avidly eat plant parts containing seeds (catchfly *Silene,* anemone, double buttercup, chervil, cow 510 parsnip, *Pedicularis,* and others). Thus, throughout the vegetative period chamois preferentially feed on the more nutritive portions of vegetation (I.V. Zharkov).

In the latter half of August, 1957 in Zakatal' preserve, chamois quite often grazed in meadow areas slightly below the forest level and in open meadows in the subalpine belt of mountains (up to 2,400 m). They grazed most avidly in humid ravines and around rocks where vegetation was more succulent. Over 50 species of herbaceous plants and one fern were recorded as consumed by chamois; up to 75% were species consumed well in Caucasian preserve. Chamois showed a noticeable preference for upper parts of plants, nibbling the tops of umbellifers (cow parsnip, golden chervil, Caucasian caraway, meadow seseli *Libanotis transcaucasica,* and others), some Compositae (cornflower *Centaurea salicifolia* and *C. fischeri,* camomile *Anthemis rigescens* and others, nipplewort *Lapsana intermedia,* dandelions, and so on), *Cephalaria gigantea, Scabiosa bipinnata,* and *Betonica grandiflora.* Also excellently consumed were sorrel (*Rumex acetosa* and others), crowfoot, Caucasian clover, bluebell, and so on. Old grazed dumps of grasses were numerous in the pastures; evidently, these belonged to the first half of summer and consisted of fescue, rye-grass *Arrhenatherum elatius,* Caucasian reed grass, bent grass, purple false brome *Brachypodium silvaticum,* and so on. Large lilies (*Lilium monadelphum*) were noticed a few times; chamois nibbled at their leaves and the upper portions of the stalks with flowers (Zakatal' preserve).

In some sections of pastures chamois consumed only one type of plant, for example *Cephalaria gigantea,* the flowers of which were bitten off; other species of plants, usually well consumed, were untouched. Quite often the preferred species was reached under the canopy of other taller plants, which is particularly characteristic of forest pastures. All this creates the impression of high food selectivity in chamois (A.A. Nasimovich and I.F. Popkova; A.I. Shreter).

In winter chamois consume large quantities of grasses in the dry as well as green state. Of particularly great importance are mountain fescue (it remains green in winter) and sheep's fescue. In spring in mountain meadows stalks of common whortleberry are well consumed (Zakatal' preserve). Whereas in summer chamois consume only a small quantity of tree and shrub foods, thin branches, shoots, and buds of some deciduous varieties are consumed in winter and early spring; mountain ash, willow, beech, and some others serve as auxiliary food of no small importance; they seek and avidly consume leaves and shoots of blackberry and even mistletoe (Nasimovich, 1949). In Zakatal' preserve (Rychegel' range, upper forest limit, 1957), chamois consume well in this time of year shoots of oak *Quercus macranthera,* Trautvetter's maple, and viburnum *Viburnum lantana,* and nibble at the thin branches of dog rose, Caucasian honey-suckle, meadowsweet *Spiraea crenifolia,* and usually enter into the subalpine mountain belt for whortleberry (A.A. Nasimovich and I.F. Popkova).

In winter chamois also consume needles of pine and fir (Dinnik, 1910), strands of lichen *Usnea barbata,* and quite often moss from the trunks of trees (Nasimovich, 1939). In forest regions chamois feed in autumn on fallen chestnuts and acorns (Markov, 1938; and others).

In the snowfree period of the year chamois visit salt licks, sulfur and other springs containing mineralized waters, and lick argillaceous soils, breaking up the turf with their hooves for this purpose; quite often, they consume moraine clays and visit artificial solonetzes [salt-impregnated soil] and salt licks (Nasimovich, 1938).

Home range. Irrespective of whether chamois live in relatively small groups or large herds, the dimensions of the home range of a herd varies widely, from 100 to 200 to 1,000 hectares or sometimes even more, while the extent of daily travel ranges from one to several kilometers. In alpine meadows of the western Caucasus the range of daily wanderings of chamois does not usually exceed 4.0 to 5.0 km, and in general is much less than in tur; in the forest zone the home range of chamois is even less (Nasimovich, 1949). Compared to tur, 511 chamois are more attached to their accustomed places and even when constantly persecuted by hunters leave them most reluctantly; they are regularly seen in their favorite pastures, near salt licks, and so on. Animals living in the montane forest belt exhibit the maximum degree of permanent settlement.

Daily activity and behavior. In summer chamois graze mostly in the mornings and evenings, but compared to tur, their daily rhythm of activity is not so distinct. In the Caucasian preserve from 10:00 a.m. to 2:0 p.m., when most tur are in their beds and not more than 7% are grazing, a significant number (30–40%) of chamois graze. In the forest, where it is much cooler, the number of chamois grazing during the day can be even higher, up to 90–100% in the early morning hours. On overcast and rainy days and also around autumn, daily activity shows even less periodicity (Nasimovich, 1949; and others).

On warm summer days from 9:00 to 10:00 a.m., and on southern slopes even from 7:00 a.m., chamois leave the open alpine pastures for their beds in forests or climb slightly upwards on the slopes. The animals conceal themselves in the shadows of trees and rocks and quite often enter caves to avoid troublesome insects, or lie on snowbanks and projections on the slopes where the wind blows strongly; they usually do not go onto glaciers. Evening grazing commences from 4:00 to 6:00 p.m. (slightly later than in tur) and continues until nightfall. Chamois evidently graze for part of the night as well.

In some regions of the eastern Caucasus chamois, like tur, are seen in alpine meadows only early in the morning and late in the evening, and descend into the forest during the daytime and at night (Dinnik, 1912). This is also the pattern in Zakatal'sk preserve.

Chamois hooves are characterized by their great mobility, firmness, and relatively large size; along the edge there is a well-defined rim, while their underside is soft. The weight load on the hoof surface is 200 g per cm^2, i.e., roughly the same as in reindeer (Nasimovich, 1955). Chamois are extremely agile on steep rocky and grassy slopes. While descending steep slopes the metapodia of the hind and forelimbs at times grip the ground firmly (Tsedvits, 1937). Chamois move better on loose snow than tur, but when the snow is chest-deep, movement is greatly hampered. Hence on days of snowstorms and the days following, chamois stay under rock projections or close to large-branched fir trees, waiting for the snow to settle, feeding only occasionally during that period. Caucasian chamois can withstand cold well.

Olfaction and vision are well developed in chamois and their sense of hearing acute. Quite often it is possible to observe chamois at "play." Several animals run up along a snowfield and then run down, or also jump onto a huge trunk of a fallen tree and then run along it. In their bed chamois often rise and change their posture (on steep slopes some chamois sit like dogs on their hind legs). While pasturing they move from one place to another, nibbling only some plant parts (tur eat the plant more thoroughly). Chamois swim easily across mountain rivers. In the event of danger they hide on steep rocky slopes but are not capable of rapid, prolonged running.

For much of the year the animals live in herds of mixed composition. In summer groups may consist of only adult males or only females with young and juveniles. Gregariousness is maximum among Caucasian chamois in August, September, and October, and at the end of winter. The largest groups of chamois are seen in high

alpine meadows and may exceed a hundred animals, but they live in such large herds for only a few days, splitting thereafter into small groups. The herd composition is usually unstable; sometimes individual animals or small groups join a herd or move out of it. Gregariousness is minimal from end of April to May when the winter herds break up and some of the females separate for parturi-
512 tion; later, the females live in isolation for 1.0 to 1.5 months. In the forest and at places where the animals are intensely persecuted by hunters, chamois are confined to groups of five or six animals and rarely more.

Seasonal migrations and transgressions. From April to early May chamois begin to move up into the mountains, but in the event of a snowfall return to the forest for a while. In May and June in the alpine belt many chamois graze on the southern mountain slopes where food is more abundant; in July and August they often move to northern slopes, gradually ascending higher into the mountains. Some animals remain year-round in the montane forest belt. In September most descend to lower levels.

In October-November in most regions of the Caucasus nearly all of the animals abandon the alpine belt and descend into the forest, congregating on steep slopes covered with pine or deciduous forests. For wintering chamois particularly prefer rocky sections of lateral river valleys and regions in the zone of "snow shadows" under the protection of "mountain screens" which restrict much of the precipitation to one slope. In winter a particularly large number of animals are seen in sunny sections but they are not rare on shaded slopes. Most animals winter in the mountains at altitudes from 1,200 to 1,700 m and only stray animals are seen in alpine meadows in winter. Chamois live in winter in rather small isolated groups. In snowy parts of their range the distance covered during seasonal migrations often exceeds 20 to 25 km (Caucasian preserve, Abkhaziya, Svanetiya, Rachin, and Adzharo-Imeretin ranges), while the vertical extent of migrations attains 1,500 m. In the forest belt some of the animals hardly migrate at all. In January–February in the western Caucasus intense snowfalls are quite common, during which many chamois descend even lower (Nasimovich, 1939, 1949, and 1955). Seasonal changes in the life of chamois in the Little Caucasus have hardly been studied.

Reproduction. Rut in chamois commences in the last 10 days of October,[135] extends into November, and ceases at the end of

---

[135] According to Ekvtimishvili (1952) in Lagodekh preserve rut in chamois commences in mid-October. This is evidently incorrect. Markov (1938) states that it occurs in November in this region.

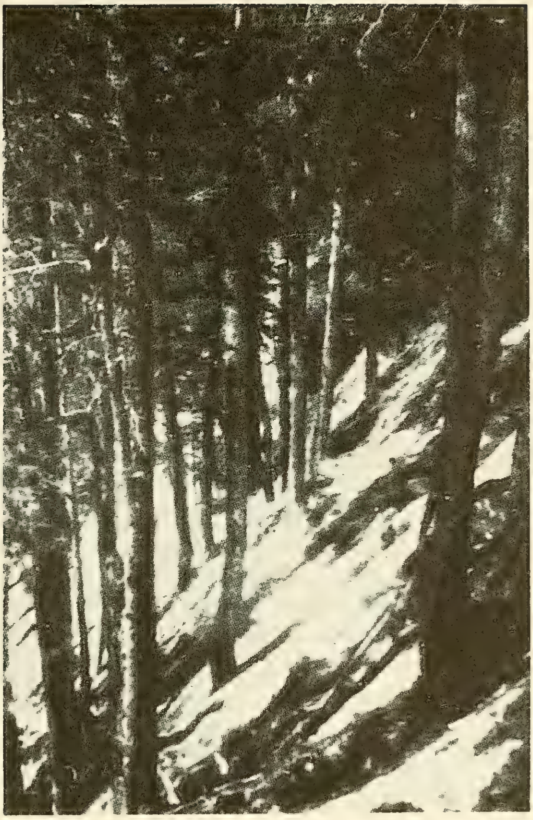


Fig. 167. Winter habitat of chamois on southern slope of Gefo mountain, 1,600 m above sea level. Caucasian preserve. February, 1935. Photograph by A.A. Nasimovich.

November or, in the event of late commencement of rut, even in early December. As the period of rut approaches particularly large herds of chamois usually split into much smaller groups (Dinnik, 1910; Nasimovich, 1939). However, on the contrary at places where the population is not large herds merge into larger groups and break 513 up only in December. Chamois remain extremely mobile throughout November, often emitting a muffled bleat. Males often chase each other and sometimes skirmishes occur while chasing away competitors. Dinnik (1910) relates an instance of a male pushing a rival over a precipice, but such episodes in chamois combats are rather rare. In the period of rut mixed groups (two or three adult males, five or six adult females, and some juveniles of both sexes) and small harems of one male and half-a-dozen or more females are seen. The male mates with the same female several times (Caucasian preserve).

Behind the horns, close to their base, paired glands occur in both sexes which enlarge during the period of rut. They exude a strong musky odor in the male, stimulating readiness for coitus in the female (Couturier, 1938).

Female chamois mature in the second year, but bear their first offspring only in the third. Males start breeding at the age of three or four years since, at an earlier age, they cannot successfully compete with older males, who drive them out of the herd (Couturier, 1938; and others).

The normal duration of gestation in chamois is 160 to 170 days (Couturier, 1938). Parturition of Caucasian chamois occurs in less accessible places, in the forest, from around April 20 to mid-May or sometimes probably even later.[136] In the Caucasian preserve the earliest date young chamois was encountered has been April 23 (1925, 1948, and 1949). Usually only a single kid is born and rarely two; triplets have not been reported in the Caucasus.

Growth, development, and molt. Chamois kids stand up two hours after birth (Krammer, 1957) and follow their mother everywhere by the second or third day. They suckle frequently (Inyakova, 1957). Lactation extends until the end of summer. They begin to feed on green fodder at the age of one month. Three kids aged three to five days (Teberdin preserve) weighed 2.8 to 3.2 kg. Two young chamois held in a pen in the same preserve (a male and a female) by the end of October of the first year weighed 17.2 and 21.2 kg, by the end of May of the next year 25.4 and 26.0 kg, respectively,[137] and at 1.5 years 30 kg, (N.M. Malinko). At the age of three years Caucasian male chamois weigh 38 to 43 kg, and females slightly less.

Tiny horns in the form of black pointed cones of 2.0 cm height become visible in young chamois in August; by the following spring their length reaches 5.0 to 6.0 cm and by 1.5 years 12 to 14 cm. In their second year the horn tips begin to bend (Dinnik, 1910; and others). Kids remain with their mother up to 1.5 years, or sometimes even longer.

At the beginning of winter the dark-colored wool of adults gradually fades and the tips of the guard hairs start fraying. In April the old hair begins to shed and the chestnut-colored summer hair begins to grow underneath. Molt peaks in May but does not proceed evenly in all animals. Most adult males, and females without young, molt in early June; in females which have given birth and in yearlings molt often ends only in mid-June or even later. Emaciated and sick animals often retain their winter coat right up to the first half of July.

---

[136] Western European chamois usually give birth from mid-May through mid-June. The earliest case of parturition (unusually rare) occurred about April 1 and the last in mid-July (Couturier, 1938).

[137] In nature young animals gain almost no weight in winter.

Underfur appears at the end of August and winter guard hair begins to grow later; summer hair is not shed but preserved right up to the following spring. The light chestnut color of summer hair turns grayish-brown around August 20 and blackish-brown in September. The first to sport a winter coat are adult males, during October (earlier in high mountains and later on lower slopes), but the guard hair continues to grow right up to December. By then the guard hair is roughly three times longer than in summer.

The maximum life span attained by western European chamois is 15 to 18 years, or 25 years in exceptionally rare cases. In captivity instances are known of survival of chamois up to 17 years (Couturier, 1938). Most chamois die much earlier, rarely surviving beyond 10 years.

514 *Enemies, diseases, parasites, mortality, competitors, and population dynamics.* Wolf and lynx are more dangerous to chamois than any other predators. Chamois remains were found in 11.7% of wolf feces examined in Caucasian preserve (Teplov, 1938). Wolves inflict utmost damage to chamois in open pastures with relatively gentle slopes. Chamois are almost inaccessible to wolves in rocky places and on steep slopes. From 1933 to 1937 in Caucasian preserve instances of attack of chamois by lynx were evidently very rare (A.A. Nasimovich). Recently, however, as a result of the growth of the lynx population, attacks have become a common phenomenon. In an analysis of 136 samples of food of lynx in Caucasian preserve from 1950 to 1954, chamois remains were found in 17.6% (maximum in the winter—spring period at 26%) (Kotov, 1958). Dinnik (1910) considered leopard one of the more dangerous enemies of chamois. At present, however, leopards are extremely rare in the Caucasus and cannot damage the chamois population. In montane pastures chamois can be seen grazing in the immediate proximity of bear; the latter neither attacks them nor do the chamois try to run away. In spring bear harassment of chamois is wholly possible (Nasimovich, 1940). Adequate information is not available on attack of chamois by lammergeier, golden eagle, or other predatory birds.

Chamois suffer from hoof-and-mouth disease, Siberian ulcers, necrobacillosis, tuberculosis, brucellosis, infectious keratoconjunctivitis (sometimes widespread in the Alps; Bouvier et al., 1957), coccidiosis, and some other diseases, most of which are common to long- and short-horned cattle. In the western Caucasus, through transmission from cattle, epizootic hoof-and-mouth disease has occurred among chamois, causing high mortality (Dinnik, 1909 and 1910; Nasimovich, 1949; and others).

Alpine chamois (and evidently also Caucasian) are infected by *Demodex caprae,* which parasitizes hair follicles (this infection is sometimes erroneously labeled scabies). Epizootic *Demodex* infections time and again have caused high mortalities among chamois in the mountains of western Europe (Couturier, 1938; and others). Scabies in Alpine chamois, causing emaciation or sometimes even death, is caused by the mite *Sarcoptes* (*Acarus*) *rupicaprae* (Couturier, 1938; Bokh, 1957; and others). The summer distribution of chamois on mountain slopes, their daily migrations, selection of bedding sites, etc. are greatly influenced by the presence of horseflies, midges, and other dipterans.

Sixteen species of helminths (12 nematodes, 3 tapeworms, and 1 fluke) have been detected in chamois of the Caucasian preserve. Judging from the 14 animals examined, the extent of invasion was 100%, while the intensity was 606 helminths per animal. One instance of hemorrhagic pneumonia was observed against the general background of parasitic nematodosis caused by *Cystocaulus nigriescens.* Helminths most pathogenic to chamois are *Neostrongylus linearis* and trichostrongylids of the abomasum. Echinococcosis of the liver has been diagnosed in two chamois and cysticercosis of the abdominal cavity in another two (D.P. Rukhlyadev). Chamois also suffer from coenurosis. Helminthic infection quite often results in chamois death. Of the 16 species of helminths detected in chamois in Caucasian preserve, 15 are also found in domestic animals. Chamois are infected most by helminths in regions where cattle graze (D.P. Rukhlyadev). In the Alps chamois mortality is often due to verminous bronchitis caused by the lung nematode *Protostrongylus rufescens* (Bouvier, 1947; cited from Boev, 1957).

In winters of abundant snow chamois sometimes find themselves in biotopes less suitable to them and hence fall victim to wolves. Yet instances of death of chamois due to starvation in such years are not known in the Caucasus. Instances of death of chamois caused by avalanches have increased in extremely snowy winters, for example in 1910/11 and 1931/32 (Western Caucasus; Nasimovich, 1939).

About one-half of all of the plants consumed by chamois also serve as food for tur. Evidently the similarity of diet of the animals is one of the main reasons for their generic antagonism between these species; the species are almost never encountered together in mon-
515 tane pastures. In the Caucasian preserve the population of chamois in the mountains is usually inversely proportional to the number of

tur present there, and this phenomenon cannot be explained in many cases as due to differences in the habitat requirements of chamois and tur. It is highly remarkable that in some mountain massifs, where at present tur are abundant and chamois few, the ratio of these populations 50 to 60 years ago was the other way around (Bol'shoi Bambak and Dzhuga). In regions where tur are abundant, the chamois population usually registers no perceptible increase (Zharkov, 1940; Nasimovich, 1941; and others).

Cattle, and especially sheep and goats, are also among the serious competitors of chamois. In the western Caucasus of the 108 species of plants consumed by chamois, about 30% are well consumed by horses and cattle and over 40% avidly eaten by sheep and goats. At the same time chamois consume only 9 of the 32 species of classes I and II of food plants eaten by domestic animals (I.V. Zharkov).

The rapid population reduction of chamois in the Caucasus has been promoted by their conservatism with respect to accustomed habitat. If tur are frequently threatened by hunters or cattle, they usually move away to other ranges, while chamois hold rigidly to their old places, which ultimately leads to their destruction (Nasimovich, 1941; Enukidze, 1953).

At the time of parturition of chamois cold weather often sets in again and hence many kids die within the first few days of birth. Based on long-term data for Caucasian preserve in June kids comprise an average of 17% of all chamois encountered, which drops to 12% by the end of summer (Nasimovich, 1949). According to Teplov

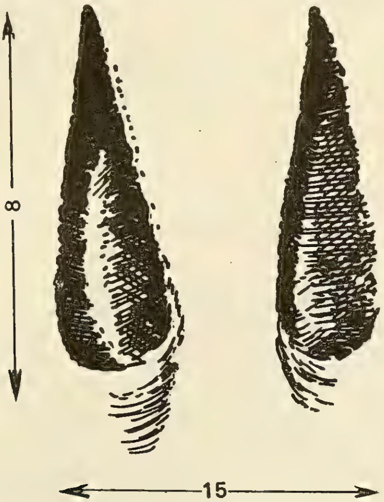


Fig. 168. Hoofprint of chamois on wet clayey soil (reduced). Pshekish Mountain. Caucasian preserve. September, 1937 (from Formozov, 1952).

(1938), by the end of July over 70% of female chamois lose their kids. The sex ratio in the population of Caucasian chamois has not been studied.

Field characteristics. The light build, shape and black color of horns, the bright chestnut color of the summer coat and the blackish-brown color of the winter coat, the prolonged hissing whistle, etc., serve as reliable features for differentiation of chamois from tur (see description of tur). The hoofprints of chamois are quite easily distinguished from those of other animals (Formozov, 1952). The feces of chamois are in the form of small longitudinal pellets (1.0 to 1.2 cm × 0.8 cm), much smaller than those of tur and bezoar goats. Trails exclusively used by chamois are narrower and less deeply formed (often not into the earth) than those of tur.

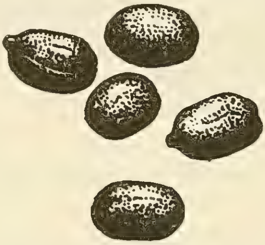


Fig. 169. Feces of chamois (natural size). Caucasian preserve. November, 1950. Sketch by T.L. Savranskaya.

Under field conditions it is difficult to distinguish males from females. Horns of the latter are thinner, shorter, and usually set more widely apart at the base, and in most cases are also less strongly curved than in males. At the end of summer, when the kids begin to grow, they are difficult to distinguish from those born in the previous year, not only in size but also in coloration, which is darker in the former. (A.N.)

Economic Importance

Hunting of chamois is mostly a sport and calls for much skill and patience on the part of the hunter.

Vereshchagin (1947) placed the annual catch of chamois in the Caucasus at 1,500. At present chamois hunting is prohibited almost
516 everywhere (Georgia, Azerbaidzhan, and others); nevertheless the animals continue to be hunted (control of hunting in the mountains is extremely difficult). Chamois are most often hunted by stalking, more rarely by lying in wait for them on their trails or at salt licks, or by chasing. As a result of the resistance of chamois to gunshot injur-

ies, firing from smoothbore guns [shotguns] results in a large number of injured animals.

The meat of chamois is best at the end of summer and in autumn, but even then it is tough and less tasty than the meat of other wild ungulates. The fat has a high melting point and rapidly becomes sticky in the mouth. In the period of rut the meat of males acquires an unpleasant smell, and at the end of rut males have lost all their accumulated fat. The yield of meat is mostly 15 to 25 kg or about 60% of the carcass weight. The winter hide is furry and warm but the hair coarse. It is most often used for rugs and sometimes collars. The summer hide is used for belts. Wall decorations, pegs, and walking stick handles are made from the horns (Vereshchagin, 1947; and others).

Local peoples attempted to tame chamois caught young and even obtained offspring from them (Razevig, 1905). In captivity (Teberdin preserve) many chamois have died, sometimes at the age of 1.5 months or even as adults, due to the obstruction of the duodenum by lumps of hair. The loss of hair by licking or even pulling it out of other animals was evidently the result of malnutrition, but this question has not been thoroughly studied. In Russian zoological gardens chamois are relatively short-lived.[138]

Chamois do not hybridize with either short-horned cattle or with mountain goats as erroneously stated by Chudi (1873) and several other reporters. In one of the five sheep artificially inseminated, the ovum was seen with chamois sperms wedged in its transparent membrane 30 hrs after insemination; the egg did not undergo cleavage (Lopyrin et al., 1956).

In view of the continuing reduction of the chamois population in the Caucasus their hunting in several regions should be totally banned or at least limited to September and the first half of October.[139] Caucasian chamois may find suitable areas for acclimatization not only in the Caucasus but also in Middle Asia, the Crimea, and other montane regions, as pointed out long ago by Razevig (1905). (A.N.)

---

[138] Alpine chamois held in captivity (France) often die from intestino-abdominal diseases (Bouvier et al., 1957).

[139] In Georgia and Azerbaidzhan chamois hunting is often permitted from August through December.

Genus of Mountain, or Rock, Goats[140]

Genus *Capra* Linnaeus, 1758

1758. *Capra*. Linnaeus. *Syst. Naturae,* 10th ed., vol. 1, p. 68. *Capra hircus* Linnaeus (domestic goat).

1762. *Hircus*. Brisson. *Regn. Anim.,* p. 12. *Hircus* Brisson = *Capra hircus* Linnaeus.

1776. *Ibex*. Pallas. *Spicil. Zoolog.,* vol. 2, p. 52. *Ibex sibiricus* Pallas.

1795. *Aries*. Link. *Zool. Beytr.,* vol. 1, no. 2, p. 96. Replacement for *Capra*.

1811. *Aegoceros*. Pallas. *Zoogr. Rosso-Asiat.,* vol. 1, p. 114. *Capra hircus* Linnaeus.

1905. *Orthaegoceros*. Trouessart. *Catal. Mammalium. Suppl.,* p. 738. *Capra falconeri* Wagner.

1916. *Turus*. Hilzheimer. Brehm's *Tierleben. 4 Aufl. Säuget.,* vol. 4, p. 273. *Capra caucasica* Gueldenstaedt and Pallas.

1916. *Euibex*. Camerano. *Atti Acad. Torino,* vol. 51, p. 338. *Capra ibex* Linnaeus.

1916. *Eucapra*. Camerano. *Atti Acad. Torino.* vol. 51, p. 338. *Capra*
517 *sibirica* Meyer.

1949. *Turocapra*. De Beaux. *Atti Soc. Ital. Sc. Natur. Milano,* vol. 88, p. 17. *Capra pyrenaica* Schinz.

Animals of moderate size, stout or sometimes quite heavy build, with fairly thick and powerful legs, and a typical "goat-like" appearance.

Metacarpals (compared to those of genus *Ovis*) relatively short and thick (diameter of diaphysis exceeds one-tenth length of bones).

Facial part of skull normally developed. Part of skull behind horns relatively elongated. Anteroparietal region highly curved. Skull pneumatized rather significantly. Ethmoid pit absent or weakly developed. Nasals of normal structure and articulate with frontal, lacrimal, maxilla, and premaxilla. Ascending processes of premaxillae long and wedged between nasal and maxilla or adjoin them. Nasal opening not enlarged and lacrimal of normal structure and position (does not reach nasal opening). Lacrimal depressions absent; sagittal crest absent. Infraorbital fossa large and with an indistinct anterior margin. Basal part of core of horns not elongated, i.e., distance from edge of horn sheath to upper end of orbit less than vertical diameter of orbit. Profile of skull behind horns bulging. Coronal suture does not usually form a distinct forwardly directed angle, but is more or less straight or forms an indistinct angle. Crests on parietals are very close (the least distance between them is usually less than the length of the parietals along the midline).

---

[140] In recent times mountain goats have frequently been referred to, for some unknown reason, as capricorns [animals with goatlike horns]. There is no basis for such a distortion of the well-accepted Russian name. These are not capricorns, i.e., certain animals with the horns of goats, but true goats.

Dental formula:

$$i\frac{0}{3},\ c\frac{0}{1},\ pm\frac{3}{3},\quad m\frac{3}{3} = 32.$$

Posterior and middle vertical ridges not developed on outer surface of upper premolars.

Horns of males large and massive, usually scimitar-shaped, and bent backward in a single plane. In some species they run initially up and sideways and at the tip inward and up, i.e., they form something like a part of a very gentle spiral (heteronymous bend of horns; see pp. 875–76) or are twisted fairly steeply (also heteronymous) into a spiral (in the form of a screw); the main axis of this spiral is straight. Horns circular in section, more or less triangular with a flat front surface, lens-shaped, or drop-shaped. On anterior surface or ridge of horns tubercles occur, or anterior surface fairly smooth, or ribbed, or with irregular transverse knobs. Keratin invariably black. Horns of females very small, straight, slightly turned back, and laterally compressed.

Muzzle normal (not swollen or elongated in the form of a proboscis) with no bare area at the tip. Nostrils set forward. Preorbital, inguinal, and carpal glands absent. Hoof [interdigital] glands absent or seen only in some species (*C. ibex* and *C. pyrenaica*) and only on the forelimbs. Lower surface of tail of males with special glands which exude a specific pungent odor (goaty odor). Tail triangular in cross section with a flat, bare undersurface; its length together with tassel is more than that of the ear; caudal vertebrae vary from 9 to 13.

Pelage usually uniform in length and relatively short (not shaggy). Males with well-developed beard, sometimes fairly long, on chin. Hair on lower surface of neck and on chest extremely long and forms a mane, which is very luxuriant in the winter coat. Color usually monotone, dark brown or gray, in some cases with significant light-colored areas and dark- and light-colored patterns on limbs. Sharp seasonal dimorphism seen in density and length of fur and sometimes in coloration also. Sexual dimorphism fairly distinct; females smaller, with small and simple horns, without beard and mane, or with these structures only poorly formed, and without caudal glands. Teats two (with two additional, rudimentary ones).

518 Montane animals associated with rocky, usually extremely steep sections, for the most part found at considerable, often extreme, heights, but nevertheless also found at very low levels in some parts of their range (at sea level or almost so). They usually live in small groups but some species sometimes form quite large associations.

The geographic range of the genus (Fig. 170) covers the montane regions of southern Europe, northwest Africa, the Near East and Middle and Central Asia, and northwestern India. Goats are found (reconstructed range) throughout the Iberian Peninsula, in the Alps,[141] on the islands of the Grecian archipelago (Cyclades and southern Sporades),[142] in Crete, the mountains of Asia Minor (in any case, in the Taurus and at least the Bulgar-Dag), the Caucasus, the mountains of Iran, Afghanistan, and Baluchistan. In Middle Asia they range north to the Bol'shoi Balkhan, the Kirgiz range (absent in Karatau) and the Tarbagatai, in the Altai, Sayans, mountains of northern Mongolia and Kashgariya (eastern Tien Shan), the western part of the Kunlun (evidently excluding Keria range), in the Karakoram, the Himalayas from Kashmir east to Kumaon, including also the northern Punjab, in the western Sind, in the southeastern, southern, and southwestern parts of the Arabian Peninsula, including Hadhramaut, in the Syrian region of the United Arab Republic, Palestine, the Egyptian region of the United Arab Republic (northward almost to Cairo), in northern Eritrea, the Sudan, Nubia, and Ethiopia (Simien).[143]

519 The range is divided into several regions conforming to the disposition of the montane regions, which are, in some areas, very strictly isolated from each other. Goats are capable of surviving at extremely low altitudes in suitably rugged terrain and their range in the remote past was generally not so fragmented. In some places goats became extinct (often not so long ago) and the natural discontinuity between individual regions was thus artificially magnified.

---

[141] Goats were absent in the historic period in the Balkan Peninsula. At present only acclimatized animals are found (at a single place in Yugoslavia), which evidently are not wholly pure because of hybridization with domestic forms. In the Carpathians also goats are absent at present, but they evidently survived there in the prehistoric period (Harper, 1945).

[142] References to the northern Sporades (Yioura—"Giura") probably pertain to domestic animals which have become feral.

[143] Information about the occurrence of goats in Nepal or even Sikkim is not reliable. According to the latest data they are absent in Nepal.

In the African countries listed goats are (were) encountered only from desert uplands east of the Nile valley to the shore of the Red Sea.

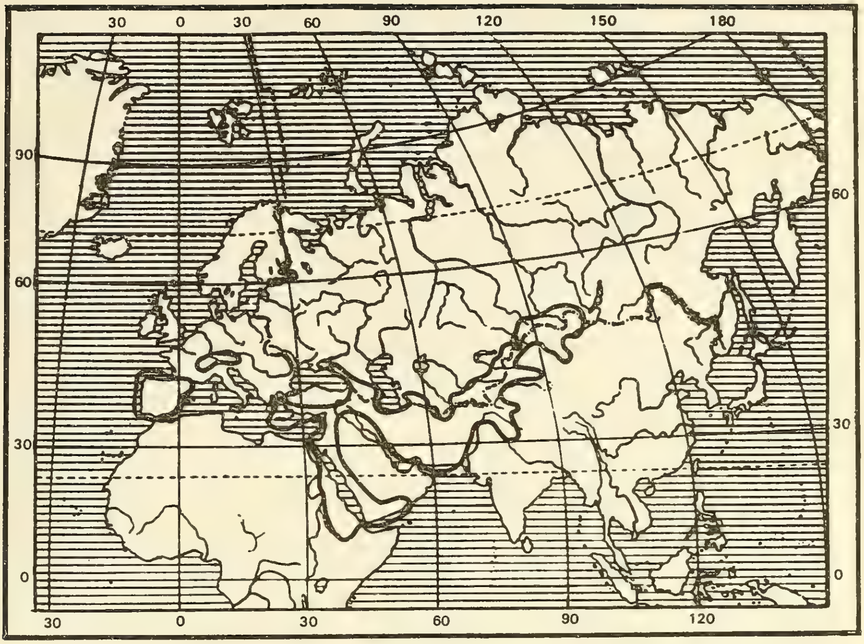


Fig. 170. Geographic range of mountain goats *Capra* L. (restored; eastern part, see Fig. 182). V.G. Heptner.

In a zoogeographic sense goats probably should be considered a Near Eastern group.

Genus *Capra* represents a fairly well isolated group but its relation to other genera of the tribe is quite close (closer than relations between genera of the tribe Rupicaprini). This is particularly true of its relation to genus *Ovis* (sheep). Typical members of the two genera (*Capra* and *Ovis*), interpreted in the usual, narrower sense, are well differentiated, and zoological differences between "goats" and "sheep" are quite apparent. Yet, because of the diversity of goat species and the exceptionally wide and deep geographic variation among both species of sheep, diagnosis of these genera is difficult. Features differentiating them (see the characteristics given here) are sometimes none too exact and vary geographically, by sex and age, etc. For example, in spite of sharp differences in the horn structure of these two groups, some individual forms in each are highly similar and essentially identical (Pyrenean goats and Dagestan tur—*C. pyrenaica* and *C. cylindricornis*—and Asiatic sheep of the *ophion* group). The question is further complicated by the fact that Central Asiatic blue sheep and African maned [Barbary] sheep, usually separated into two genera—*Pseudois* and *Ammotragus*—occupy an essentially intermediate position between the genera *Capra* and *Ovis* in several features or combinations of them. For example, Barbary sheep have caudal glands typical of goats but do not have interdigital glands, and so on. Understandably taxonomic views are highly diverse. The generic rank of each form is set aside by some authors and they are regarded essentially as goats with some features of sheep, while other authors include them in genus *Ovis*, assigning them the status of subgenera only. These forms are treated here in the traditional manner, as distinct genera, although the idea of their inclusion in the single genus *Ovis* has much to commend it. Based on the peculiarities of Barbary and blue sheep, however, the unification of genera *Capra* and *Ovis* in a single genus appears premature and hardly rational.

The position of the genus *Hemitragus* (tahr) is more isolated although it also exhibits features very similar to those of goats; its generic independence is generally acknowledged. At the same time *Hemitragus* exhibits features similar to those of the Rupicaprini, which somewhat link them with Caprini. It represents the least typical form of Caprini, beginning the series, which ends with genus *Ovis* (sheep).

Fossil material of *Capra* is sparse and does not permit a judgment about the origin and relations of the genus. It is known only from the Lower Pliocene of Europe and Asia from the region of its present-day range or close to its present boundaries. Goats were found in England and Ireland in the past. Extinct genera of the tribe are known from the Lower Pliocene.

Fossil goats belong either to extant species or to one or several extinct species, of which the best known is *C. prisca*. The latter is close to the present-day bezoar goat, *C. aegagrus*, and probably not a separate species but only a form of the latter.

Attempts have been made time and again to assign various (in fact, all) species to independent generic status (see synonyms above). Such attempts are futile since to give even subgeneric status to these names is impossible. An exception might be made only for the markhor *C. falconeri*, which stands apart among the remaining
520 species in form and curvature of horns and certain other features (neck tress). Therefore, there are only two subgenera—*Orthaegoceros* Trouessart, 1905 with one species, *C. falconeri*, and *Capra* Linnaeus, 1858, with all the remaining species.

Unlike most cavicorn groups (and ungulates in general) where taxonomy, as far as it relates to species composition has been greatly revised and simplified, the question of the structure of genus *Capra* still continues to evoke diverse opinions. The main taxa, i.e., species or groups of races, within the limits of the genus are quite distinct and the whole question revolves around their arrangement and grouping. In the last few decades the fairly clear picture of these taxa has become confused because attempts of several authors to combine and reduce the number of species, leading to an unnatural classification. Some of the new systems of classification are indeed a step backward, all the more so because some regroupings of species have not been based on a study of even craniological features, let alone new morphological, paleontological, or other such data; but rely mainly on a combination of already known features of horn structure, color, etc., frequently ignoring or undervaluing zoogeographic and biological data.

The abundance of forms of this group that we have [i.e. in the Soviet Union] (a majority) compels me to examine the structure of the genus in greater detail. Lydekker (1913) included nine species in the genus; central and east Caucasian tur, *C. caucasica* (including *C. cylindricornis* as a subspecies); Kuban or western Caucasian tur, *C. severtzovi*; Pyrenean goat, *C. pyrenaica*; Siberian goat, *C. sibirica*; Nubian goat, *C. nubiana*; Abyssinian goat, *C. walie*; bearded or bezoar goat, *C. hircus*; and markhor, *C. falconeri.*[144]

Schwarz (1935) regarded markhor as a distinct genus and included in genus *Capra* only one species, *C. ibex,* in which 11 forms were combined, all formerly recognized as species or subspecies. Two groups were recognized within this species. The "northern" group of *ibex* included three (!) Caucasian tur—*severtzovi, caucasica,* and *cylindricornis,* alpine (*ibex*), Pyrenean (*pyrenaica*), and Siberian (*sibirica*) goats. This group is characterized by horns having a broad frontal surface with knobs, and white spots on the forelegs either faint or absent. The "southern" group of *hircus* included Sinai goat (*sinaitica*), the Baluchistan form of the bezoar goat (*blythi*), the nominal form (*aegagrus*), the Nubian goat (*nubiana*), and the Abyssinian goat (*walie*). In this group spots on the legs are distinct and a tendency toward keel formation on the front surface of the horn is evident. This scheme of classification is of course quite unsatisfactory and unacceptable. Ellerman and Morrison-Scott (1951) have recognized five species: bezoar goat, *C. hircus*; alpine ibex, *C. ibex* in which they include Nubian goat, *C. nubiana,* Kuban (western Caucasian) tur, *C. severtzovi* and Siberian ibex, *C. sibirica*; central and eastern Caucasian tur, *C. caucasica* (*C. cylindri-*

---

[144] The Latin terminology given here is that used by the authors cited.

cornis is considered a synonym); Pyrenian goat, *C. pyrenaica;* and markhor, *C. falconeri.*

If the *nubiana* group can be annexed to the species *C. ibex* based on purely morphological considerations, then the inclusion here of Siberian ibex (*C. sibirica*) and Kuban (western Caucasian) tur (*C. severtzovi*) is unacceptable from both systematic and zoogeographic considerations.

Heltenorth and Trenze (1956), having accepted the general scheme of earlier taxonomists, proceeded a step forward by logically linking the Caucasian tur, *C. caucasica* (*cylindricornis*) to the species, *C. ibex*. They thus recognized four species in genus *Capra* (*pyrenaica, ibex, aegagrus,* and *falconeri*). Finally, and most recently, some taxonomists have accepted a single species, *ibex,* containing all goats including even the markhor, *C. falconeri,* thus proceeding even farther than Schwarz (1935). Such "groupings" have little to do with systematic analyses and should not be taken seriously.

521 In the present state of our taxonomic and zoogeographic knowledge evidently it would be more natural to include the following eight species in the genus: Pyrenian, *C. pyrenaica;* alpine, *C. ibex;* bezoar or bearded, *C. aegagrus* (*C. hirus*); Nubian, *C. nubiana;* Kuban or western Caucasian, *C. caucasica;* Dagestan, *C. cylindricornis;* Siberian, *C. sibirica;* and markhor, *C. falconeri.*

This scheme and grouping of species is tentative and the entire question of species composition of genus *Capra* requires special consideration, for which there is no place here. The following points, however, briefly substantiate the grouping adopted. All goats are very close to each other in craniological and other features. All species apart from the bezoar *C. aegagrus* are strictly allopatric. *C. aegagrus* in the eastern part of the Great Caucasus lives together with the Dagestan tur, *C. cylindricornis,* without interbreeding. The ranges of the Nubian ibex, *C. nubiana* (Syria, Arabian Peninsula, and northwestern Africa), and the alpine ibex, *C. ibex,* are separated from those of the bearded goat, *C. aegagrus.* Both species of tur in the Caucasus are very close and placing them in different groups (*ibex* and *caucasica*) is irrational. They are nevertheless quite distinct. Assigning the Siberian (Central Asiatic) *C. sibirica* to the Alpine species, *C. ibex,* also requires special examination; its range is separated from that of *C. ibex* by the ranges of the bezoar goat, *C. aegagrus* (and partly perhaps, by markhor, *C. falconeri*) and the ranges of the Caucasian turs. If the Nubian ibex, *C. nubiana,* Caucasian tur, and Siberian goat are united with *C. ibex,* there is then no justification to separate the Pyrenean species (*C. pyrenaica*). From the viewpoint of extreme "lumping," all goats from the Pyrenees to Ethiopia and Central Asia should be placed in a single species—*C. ibex*—excluding from it only the bezoar goat (*C. aegagrus*) for reasons of its coexistence with another species in the Caucasus, and markhor, *C. falconeri,* which is well distinguished morphologically and lives in the same territory as the Siberian form. Furthermore, in an extreme case, it would be possible to combine it also with *C. ibex.* Strictly speaking, its differences from some other species are somewhat greater than the differences between, for example, the Dagestan tur, *C. cylindricornis* and the Siberian form, *C. sibirica.*

The mountain sheep, *Ovis ammon,* with its extreme geographic variation, could serve as a precedent for an extensive merger of species of mountain goats. However this analogy is superficial. In the case of *O. ammon* from Corscia to Tibet, a single group of characteristics, primarily horn structure, are morphologically as well as geographically developed very strictly, successively, and gradually. There is no such sequence whatsoever with regard to the distribution of goats (Pyrenees–Ethiopia–Caucasus–Central Asia). Suffice it to say that the horn characteristics of Pyrenean goat (*C. pyrenaica*) are seen in Dagestan tur (*C. cylindricornis*). In principle, however, this type of horn attains its utmost development in markhor (*C. falconeri*), especially, for example, in the form *chialtanensis.* Horns of the alpine (*C. ibex*) type are large in Central Asia, small in the western Caucasus (*C. "severtzovi"*), and medium in the Arabian Peninsula and northwestern Africa (*C. nubiana*), and so on.

The various forms and species of goats interbreed freely in captivity. This characteristic, however, cannot justify combining them into a single species. It is well known that in species which are sharply isolated geographically, reproductive isolation in a purely physiological sense may not arise at all, which does not interfere with their being a valid species.

Thus, the eight species listed above represent the most natural system, morphologically as well as geographically.

These eight species comprise about 36.5% of the species of the subfamily. Of these, one is Afro-Asian (*C. nubiana*), two European (*C. pyrenaica* and *C. ibex*), and the remaining five purely Asiatic. In terms of species abundance, therefore, the group is Asiatic.

Capra are game animals.

The domestic goat (*"Capra hircus"*) belong to the genus *Capra.* 523 Its ancestor was the bezoar, *C. aegagrus,* but it is possible that it is a mixture of several species (including *C. ibex* and *falconeri*) and thus had several centers of domestication.[145]

---

[145] It is interesting that at some places in the Caucasus, especially in Dagestan,

Five species are found in Russian fauna: bezoar or bearded goat, *C. aegagrus* Linnaeus, 1758; Kuban (western Caucasian) tur, *C. caucasica* Gueldenstaedt and Pallas, 1783; Dagestan tur, *C. cylindricornis* Blyth, 1841; Siberian ibex, *C. sibirica* Pallas, 1811; and markhor, *C. falconeri* Wagner, 1839. They constitute about 62% of the species of the genus and about 2.0% of species of Russian fauna.

These species are distributed in the mountains of the Caucasus, Middle Asia, and southern Siberia.

All are mountain forms confined to the more rocky and rugged, mostly highest sections of montane massifs.

Although *Capra* are game animals, they are often few in number, and protected from hunting. (V.H.)

16. BEARDED OR BEZOAR GOAT[146]

Capra (Capra) aegagrus[147] Erxleben, 1777

1777. *Capra aegagrus*. Erxleben. *Syst. Regni Anim.*, p. 260. Dagestan, eastern part of Great Caucasus.

1788. *Antilope gazella*. Gmelin. *Syst. Naturae,* vol. 1, p. 190. Nec *Capra gazella* Linn., 1758 (South African antelope). Iran.

1843. *Capra caucasica*. Gray. *List Mamm. Brit. Mus.,* p. 167. Nec Gueldenstaedt and Pallas, 1783 (Caucasian tur). Caucasus.

1875. *Capra blythi*. Hume. *Proc. Asiat. Soc. Bengal,* 1874, p. 240. Sind, northwest India (now, southeast Pakistan).

1918. *Capra hircus neglectus*. Zarudny and Bilkevitsch. *Bull. Musée*

---

among domestic goats individuals with a typical tur coat color occur.

[146] There is no popular Russian name for this species although "bearded goat" is nevertheless used. In the Kopet-Dag this species is simply called "goat". It is similarly known even in the Caucasus, distinguishing it from tur. Nevertheless some Caucasians evidently do use the term "bearded goat" (Markov, 1934). The name "bezoar goat" is a purely bookish and artificial name translated from the German language and not known anywhere to peoples of the Soviet Union. Russian and other local hunters know nothing about "bezoar," i.e., concretions of hair, cellulose, and other material sometimes found in the stomach or intestine of this species (also found in other ungulates). In the Middle Ages and even much later in Europe and some other countries, "bezoar" was regarded as a magic "stone" which increased fertility and cured cases of poisoning. In Russia it was called "bezui" or "bezui-kamen" and was credited with these very same properties. The patriarch Nikon wrote to Tsar Aleksei Mikhailovich lamenting that someone had attempted to poison him and that he was licking a "bezoar" to offset the effects.

[147] In literature this species often figures under the name *Capra hircus* Linnaeus, 1758 (*Systema Naturae,* 10th ed., vol 1, p 68) a name which Linnaeus gave to the domestic goat of southern Sweden. It is inapplicable for the reasons given above (see footnote no. 17, pp. 539–40 above pertaining to the Latin name of aurochs).

Transcasp., vol. 1, p. 12. Zarudnyi and Bil'kevich. *Izv. Zakasp. Muzeya*, vol. 1, p. 12.[148] Bendun (Bendan) on Iran-Afghanistan border in Seistan (Sistan) country immediately west of the northern part of the Hamun marshes (around 31°20′ N lat. and 60°40′ E long.).

1950. *Capra aegagrus turcmenicus*. Zalkin. Tsalkin. *Doklady Akademii Nauk SSSR*, vol. 20, no. 2, p. 325. Tava range, Central Kopet-Dag, 25 km south of Gyaurs railway station. (V.H.)

Diagnosis

Goat of moderate size with long horns curved like scimitars in a single plane with sharp knobs on the front ridge. Distinct black line occurs along the spine. Beard dense and long. Tress of long hair on neck and chest absent. (V.H.)

524 Description

Bearded goats, compared with other species of Russian goats, are moderate in size and much lighter in build. Legs relatively short but thick and strong. Neck fairly thin and long, head small, and ears short. Beard dense and long. Tail short and flat.

Horn of male very long and comparatively thin, with narrow base, and of almost identical width for much of its basal and central part. Horns curved like scimitars; at the base and midportion curvature of bend extremely gentle, at terminal one-third sharper, and horn tip turned not only back but also slightly down.[149] Horns bend almost in a single plane, in any case for much of their length; and only end portions deviate from this plane, slightly turning inward, facing each other. Sometimes, the whole horn is strongly curved in the same plane.

Horns highly compressed laterally, front ridge being extremely sharp, back rounded, and lateral surfaces slightly convex. In transverse section horn elliptical with a pointed front portion, or more accurately in the shape of an elongated teardrop. Front ridge with several knobs, sharp, and slightly elongated in vertical direction.[150]

---

[148] In this publication, page 12 is duplicated twice—in the introduction to the article and at the place where this description has been given.

[149] Sometimes horns are bent for even more than one-half of their curvature (Dinnik, 1910).

[150] The number of knobs, as in other species of goats, has no relation to age. In spite of the prevailing view among hunters, it is impossible to determine the age of an animal from the number of knobs on its horns.

Lateral surfaces slightly rugose. Annual rings distinct. Keratin blackish-gray or almost black. Overall, horns of bearded goats, though larger, appear lighter than those of other species with similar scimitar-shaped horns (*ibex* and *sibirica*). Horns set on skull very steeply (vertically) with a small angle between them. Nevertheless arrangement of horns on skull in animals of a given locality varies perceptibly. Sometimes the spread is rather large. Variability in this aspect of horn structure is evidently less, however, than in Siberian ibex (*C. sibirica*).

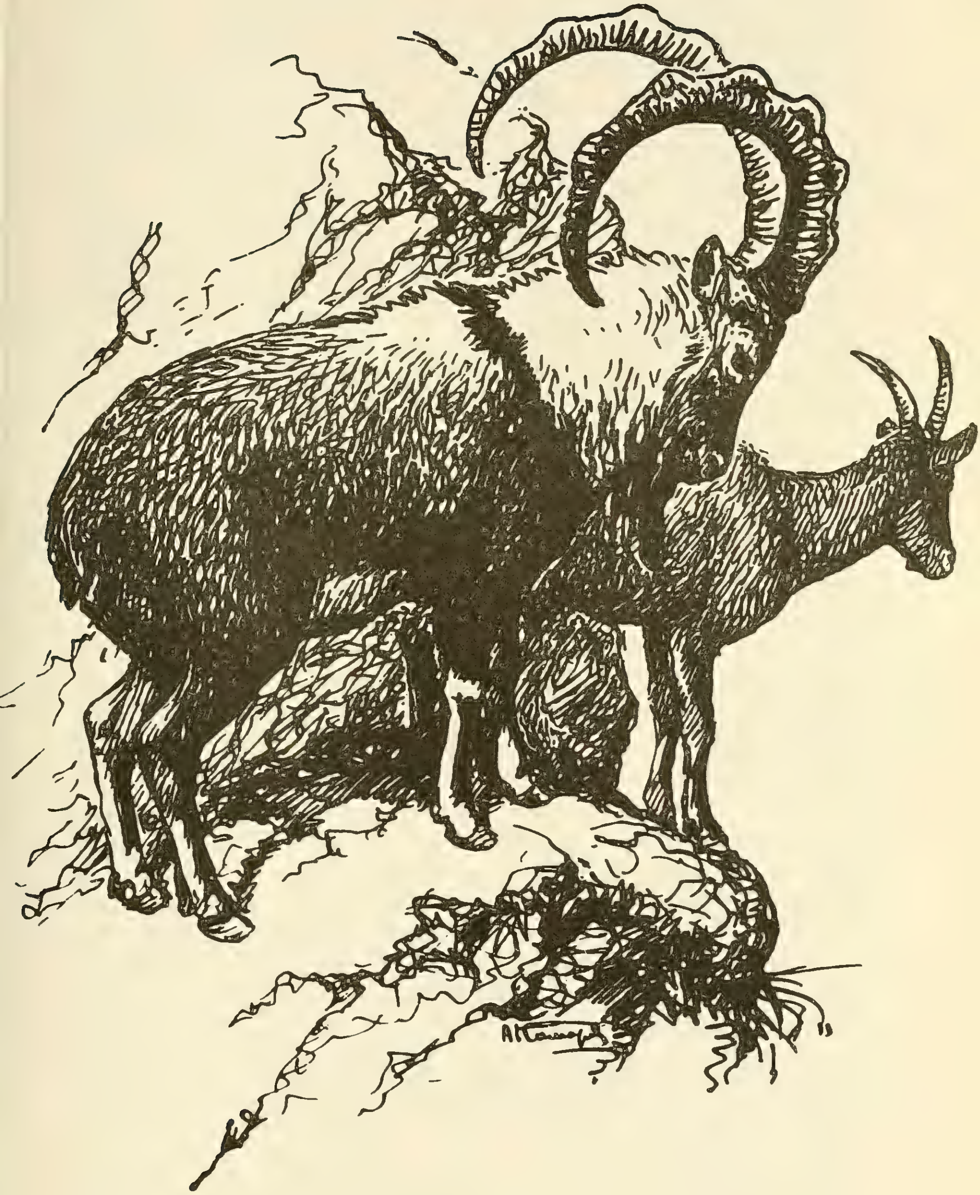
Horn of female very short and at its maximum length no longer than one-half that of male horn. Female horn thin and without knobs on front rib; the latter quite obtuse, with inner surface flat, and outer surface convex. Usually horns bent very slightly, or almost straight, but sometimes curved steeply. Relatively short horns of young males thin down rapidly from base to tip; this is because the base is almost equal in size to that of older goats. Moreover, the number of knobs on the anterior rib is less and the horn curves in a single plane.

Skull fairly slender, elongated in shape, and not broad in orbital region (about 50% of total skull length); orbits relatively small and without sharp [rostral] constriction anteriorly. Bony core of horn compressed laterally, and with a sharp anterior ridge. Prominences occur in front of base of bony core on frontals, due to which forehead concave in the middle. Nasals relatively short and project forward slightly; a perpendicular line drawn from tip of nasals to palatal surface falls short of the anterior end of the tooth row by a distance of not more than the length of the first two premolars (equal to about 4.2% of total skull length). Mastoid process relatively light. Interpterygoid fossa relatively narrow (Figs. 177, 178 and 179).[151]

"Color of back and flanks in summer reddish-brown or chestnut-brown, sometimes chestnut-gray, and in winter grayish-brown or light chestnut. A vivid blackish-brown band extends down the
525 spine. Head dark brown and coloration in front portion particularly rich and beautiful. Beard and dense coat on whole of underside of muzzle almost black. Dark brown band extends from in front of shoulder to base of neck, forming a collar. In some animals this band is narrow and weakly marked. A blackish-brown band separates brown flanks from white or chestnut-white undersurface of trunk; front part of chest and upper part of legs also blackish-brown.

---

[151] Craniological data mainly from Tsalkin, 1950 (see also description of Siberian ibex).



522 Fig. 171. Bearded goats, *Capra aegagrus* Erxl. Sketch by A.N. Komarov.

Forelegs below wrist joint variegated—black in front and white on sides and rear. Color of hind legs almost the same. Tail blackish-brown or even black. Coat coloration in females almost identical but black band along spine not distinct; dark band in front of scapula absent, wool on forehead considerably lighter, and beard absent" (Dinnik, 1910; description based on material from Dagestan).[152]

Body length of adult males up to 1.5 m; height at sacrum almost a meter, and just a centimeter or two less at withers; tail up to 20 cm long. Weight, though less than that of Dagestan tur, can reach 70 to 80 kg.

Total length of skull in males 248 to 279 mm (M 262 or 263 mm); corresponding figures for females 215 to 234 (M 224 to 227 mm) (Tsalkin, 1950). Horn length up to 100 to 110 or even 130 cm measured along curvature. (V.H.)

Taxonomy

The relations between different forms of the genus have been studied very little and then very superficially. Attention has mainly been paid to the structure and form of horns. Hence it is difficult to determine at the present moment the actual position of individual species examined here and their relations with other species of the genus. Bearded goats could evidently be considered the least specialized species. Indications of this are the relatively large (elongated) skull portion behind the horns, and the structure of the horns—their tear-shaped transverse section, absence of a smooth anterior surface, and their curvature.

The independence of the species has been acknowledged in the various schemes of classification of the genus (except Schwarz's, 1935). Biological proof of this is the coexistence of bearded goats with another species of the genus—the Dagestan tur (*C. cylindricornis*) in a large area: they live together throughout the range of the former in the Great Caucasus. It is possible that the two species differ slightly in biotope [habitat]; bearded goats are evidently confined to much lower levels, often more to the forest zone or even to a particular forest, and not to such high altitudes as tur, which are confined to meadows and high mountain cliffs (alpine zone). Nevertheless, individuals of the two species are often seen together not only in [alpine] pastures, but also lower, because tur in Dagestan often descend into the forest zone (Heptner and Formozov, 1941). Hybrids between them are absent or, in any event, hybridization is only occasional over their wide distribution. There is evidently only one reference to a hybrid caught in nature (Pfizenmayer, 1915) [see below], but even it requires confirmation. In any case, even if there are hybrids, they are very rare and some stray instances of hybridization do not bring into question the reality of the coexistence of the two species (see sika and Manchurian wapiti).

---

[152] Bearded goats are one of the least studied Russian ungulates. In museums material of this species is scanty and information in literature about its color (primarily of winter coat), size, weight, etc., sparse.

In the southeast the range of bearded goats adjoins the range of markhor (*C. falconeri*). Here, however, a definite separation is manifested. In Baluchistan the range of bearded goats runs from the west and southwest and extends in the form of a projection to the east and northeast, slightly short of reaching Quetta (Bolan Pass, south of Quetta). Markhor approach Quetta from the north (from
526 Afghanistan) and live also in the Suleiman mountains. The ranges of the two species adjoin, or almost adjoin each other, but the two are not seen together, at least not in any significant area of the region.[153]

In Badkhiz (southern Turkmenia) and in northwestern Afghanistan the range of bearded goats closely approaches the range of Siberian ibex (*C. sibirica*) and probably adjoins it, but so far no positive information about this is available (V.G. Heptner). (V.H.)

Geographic Distribution

Bearded goats are found in the Near East from the islands of the Grecian archipelago and Crete, through Asia Minor and Iran to the Caucasus, southern Turkmenia, Baluchistan, and western Sind.

Geographic Range in the Soviet Union

The range in the Soviet Union represents the northern edge of the range of the species and covers a very small portion of the territory in the Caucasus and Turkmenia.

The range in the Soviet Union thus consists of two isolated sections which are continuous in the south outside the USSR. Each of these two sections, in turn, breaks down into several individual pockets. In some cases this division into pockets is due to man (destruction and displacement in recent and remote periods).

---

[153] The horns sketched by Lydekker (1913, Fig. 45) and described by him as the form *C. falconeri chialtanensis* (a single specimen?) from the mountain massif of Chialtan near Quetta are extremely typical and do not at all resemble horns of other races of the species. They are very strongly "opened up" and, at sufficient age, form only an incomplete turn of a spiral. It is highly probable that these horns, occurring from the region of confluence of the range of the two vicariant [parapatric] species, belong to a hybrid between bearded and markhor goats.

In the Caucasus the range covers the eastern part of the Great Caucasus mountain range. In the west it does not extend beyond the Georgian Military Highway, failing actually to reach it. In the west these goats are known from the upper reaches of the Argun, including its tributary the Kiisk, and from the Pirikitel' and Tushin Alazan (source of the Andii Kois; Dinnik, 1910).[154]

In the east goats are distributed in the region of the main axis of the mountain ranges and a significant part of Dagestan falling north of this axis. They are found here along the mountains in the Andii Kois region down to Botlikh, and in the region of the Avar Kois and Karakois almost to Gunib. Farther east bezoars are found in the region of the upper reaches of the Kazikumukh Kois and Samur (Dinnik, 1910; Vereshchagin, 1947; Heptner and Formozov, 1941). The distribution of bezoar goats farther eastward is not clearly known.[155]

North of the main axis of the highlands of the Great Caucasus goats extend along the lateral mountains (Bogos, Nukatl', and others) relatively far, especially in Dagestan. In the Gunib and Botlikh regions goats have been observed 50, 60, and 70 km from the passes leading into Georgia (Dinnik, 1910; Heptner and Formozov, 1941). Goats almost fail to penetrate the southern slopes because of the characteristic topography of the eastern half of the Great Caucasus, which is devoid of lateral ranges.

The region of distribution of bezoar goats in the Trans-Caucasus is separated from that part of the range in the Great Caucasus. The Trans-Caucasian part of their geographic range is extremely complex and at places still poorly understood, especially with regard to its former outline. Here, the species occupies the Murov-Dag and Karabakh mountains, the Karabakh foothills (in particular, in Karabakh the species is confined to Deli-Dag, Kechal-Dag, and Murov-Dag), the Zangezur range up to the Araks gorge (Ordubad and other

---

[154] It is possible that they penetrate westward even farther. There is a reference to the capture of a hybrid between a tur and a bezoar at Orotskhala, in Khevsursk Aragva, southeast of Kazbek (Pfizenmayer, 1915).

[155] Dinnik (1910) thought that this goat was absent in the region of the upper reaches of the Kazikumukh Kois and Samur. Vereshchagin (1947, map) indicates the occurrence of this species in the region slightly west of the source of the Pirsagat (probably Babadag) but does not give supporting data. In the text the distribution has been shown as in "Dagestan hills and Azerbaidzhan, in the upper reaches of the Avar and Andii Kois and Samur".

527 places), the Sarai-Bulakh range, and Negram mountains near Araks between Nakhichevan and Dzholfa (Vereshchagin, 1947). The Azat River, entering the Araks south of Yerevan, evidently forms the western boundary of the range in the region between the Araks and Sevan in Armenia (Dal', 1954).

In the west the occurrence of bezoar goats has been noted in the Pambak range extending west from the northwestern extremity of Lake Sevan and in the Aragats massif northwest of Yerevan (Dal', 1954).

An isolated pocket of occurrence of these goats is found at Borzhomi, covering a large expanse in the western spurs of the Trialets and eastern Adzharo-Imeretin ranges (Pfizenmayer, 1915).

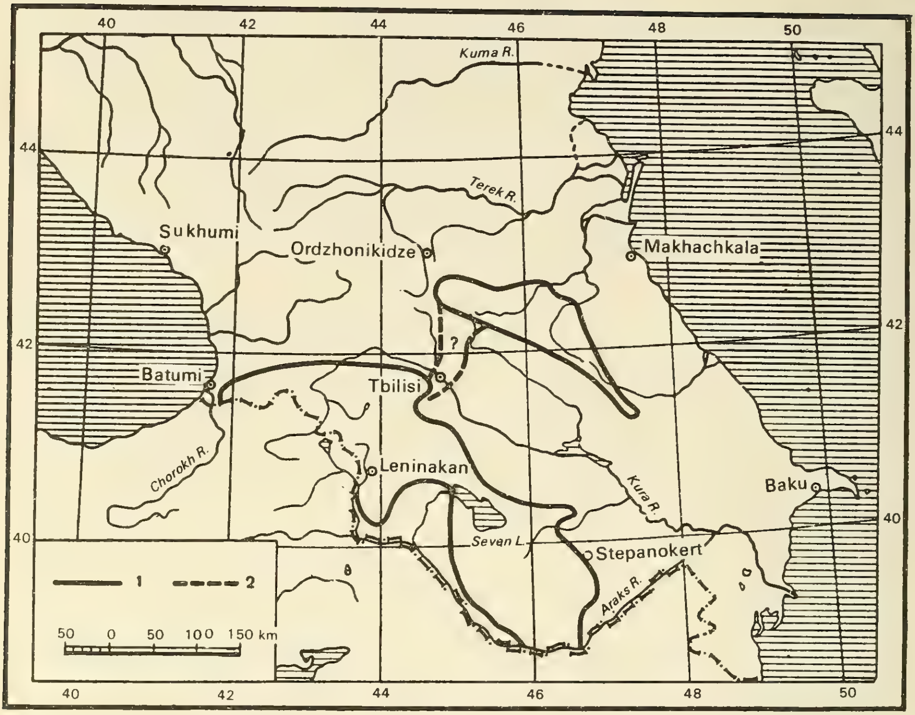
The foregoing data, pertaining to the end of the last century and first half of the present, provide a comparative picture of the geographic range. Today goats are absent only in the Borzhomi region, where they became extinct by the early 1920's.

At the same time there is no doubt that the range outlined above is very different from the natural range, or at least the range some hundreds of years ago. Unfortunately there is no concrete information available about the earlier range.

Changes in the distribution of the species under description in the Great Caucasus were not great. A somewhat wider distribution can be assumed along the mountain range in the east and north, away from its main axis. However, shifts in the range in the Trans-Caucasus are evidently very prominent. In the remote past it may be assumed that the range covered all the montane regions of Trans-Caucasus, i.e., the whole of the Adzharo-Imeretin and Trialets ranges, Papakar and Shakhdag (Sevan) ranges, and all of the region south of them right up to the state boundary. With respect to the Talyshin mountains, no concrete data are available and even material for a basic hypothesis are lacking. However, the distribution of goats there in the remote past would seem quite likely.

528 Goat distribution in the Great Caucasus and Trans-Caucasus was, of course, continuous in the past. It may similarly be assumed that they occurred in the region of the Kartalin and Kakhetin, but not the Suram ranges. However, such a distribution should be assumed only for the remote past, evidently prior to the historic period under consideration.

The range of bezoar goats in Turkmenia likewise is split into several separate pockets. The majority occur in the Kopet-Dag where the species under description is found, under suitable conditions, throughout the range within the Soviet Union, i.e., roughly from Artyk railway station (east of Ashkhabad) and almost to the north-


Kuma R.
Terek R.
Sukhumi
Ordzhonikidze
Makhachkala
Batumi
Tbilisi
?
Chorokh R.
Leninakan
Kura R.
Baku
Seven L.
Stepanokert
Araks R.
1
2
50 0 50 100 150 km
40
42
44
46
48
50

527 Fig. 172. Recent (Great Caucasus) and reconstructed (Trans-Caucasus) geographic range of bearded goats, *Capra aegagrus* Erxl., in the Caucasus.

Broken lines enclosing question mark denote region where the two sections of the geographic range possibly merged along the Kartalin and Kakhetin ranges in the remote past. V.G. Heptner.

western extremity of the range, roughly to the meridian of the Kizyl-Arvat railway station. In the south the range almost everywhere reached the state boundary.

An isolated section of the range occupies the Bol'shoi Balkhan where goats were sighted throughout the massif. A very small area of occurrence of this species is located in the Gyaz'-Gyadyk promentory along the right bank of the Tedzhen. There, goats are present in some places which directly adjoin the river (not farther than a few kilometers from it) in the stretch from the Afghan border northward to a point slightly south of Pul-i-khatun on the Tedzhen. The animals are confined here to a belt of several hundred meters, no more than 1,200 m above sea level; Kopet-Dag and Gyaz'-Gyadyk defined the outskirts of the Iranian part of the geographic range.

References by some authors to the occurrence of bezoar goats in

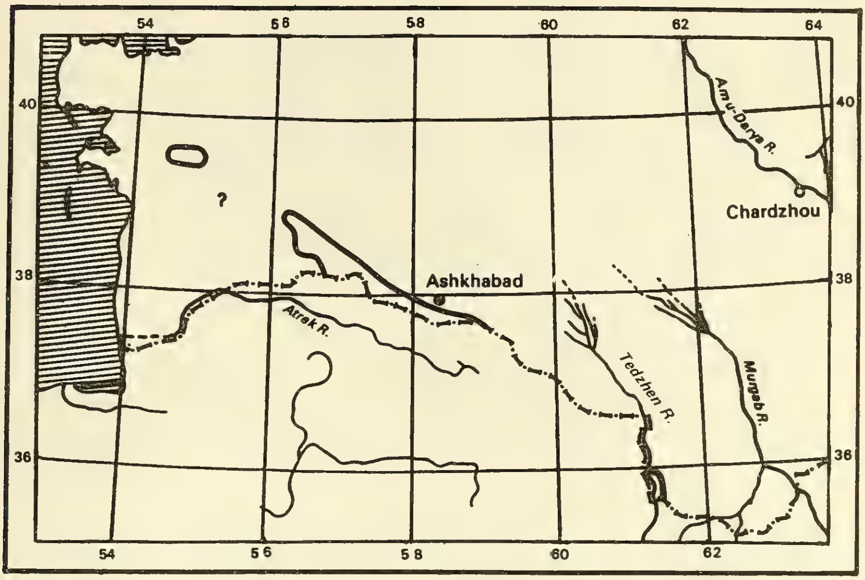


Fig. 173. Present outline of the geographic range of bearded goats, *Capra aegagrus* Erxl., in Turkmenia. Question mark refers to Malyi Balkhan. V.G. Heptner.

the Malyi Balkhan are unreliable and require proof; data on distribution in Mangyshlak and even in the Ustyurt (Dinnik, 1910) are erroneous.

The range of bezoar goats in Turkmenia at present is somewhat less than that described above. Its area shrank in the Bol'shoi Balkhan and no longer covers the whole massif. In the Kopet-Dag goats are present mainly in the much higher parts of the mountain range; the geographic range has withdrawn from the region of low and moderate heights on the northern slope. The area of occurrence of this goat has also shrunk significantly in the west and the animal is evidently no longer present west of the meridian of Kara-Kala on the Sumbar (Syunt and Khassar-Dag massifs), nor is it found south of the Sumbar, including the hills surrounding the Chandyr, which 529 enters the Sumbar. In Gyaz'-Gyadyk district the region of present distribution conforms to that shown.[156]

In 1913 bearded goats were acclimated in montane Crimea but disappeared between 1917 to 1919 (Dal', 1958).

---

[156] The range in Turkmenia is based on information available in literature but mainly on original data of V.G. Heptner.

Geographic Range outside the Soviet Union

The western limit of distribution of the species cannot be established with certainty since it underwent intense changes, not only as a result of the destruction of wild animals even at the dawn of the prehistoric period, but also probably as a result of introduced domesticated animals turning feral, also in the distant past. The range covered the islands of the Grecian archipelago—Cyclades and southern Sporades,[157] Crete, Asia Minor (in any case, the Taurus system), mountains of Armenia and the Kars region, and northwestern Iraq. From the foothills of Asia Minor the range projected in the form of an extension along the mountain ranges running along the coast of the Mediterranean Sea in the south, up to and including the Antilivan mountains (in Lebanon). The range did not reach Palestine, not even in prehistoric times (*Capra nubiana sinaitica* was there), but penetrated quite deep into the Syrian desert along the spurs of the Antilivan.

Farther east the range covered Iran (in the south including Luristan), Baluchistan in the east and northeast not farther than Quetta and Bolan Pass (south of Quetta; farther the markhor goat occurs), and western Sind.

The present boundaries of distribution of this species in Afghanistan have not been established (here, markhor are present and Siberian goat widely distributed), but there is no doubt that it occurs in an insignificant area in the extreme northwest corner of the country (at Gerirud, Tedzhen; V.G. Heptner). It probably also lives at places along the Iranian border, but evidently not in places bordering Baluchistan. (V.H.)

Geographic Variation

The number of names given to bearded goats in different parts of their range is fairly large. In fact several forms exist but only two are distinctly differentiated. In general, however, the geographic variation of the species has not been studied in sufficient material, not even for present-day animals.

Two forms are found in the Soviet Union.

1. Caucasian bearded goat, *C. a. aegagrus* Erxleben, 1777 (syn. *caucasica*).

Description given above. Overall length of skull in adult males

---

[157] References to occurrence in the northern Sporades (Yioura Island—sometimes written "Giura") evidently pertain to domestic goats which have turned wild.

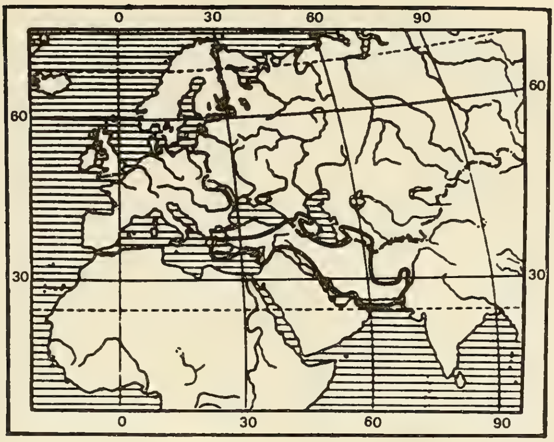


Fig. 174. Species range of the bearded goats, *Capra aegagrus* Erxl. (partly reconstructed). V.G. Heptner.

248 to 278 mm (M 263) and in females 215 to 233 mm (M 224).

Horns large and relatively massive with a fairly broad base. Circumference of horns at base 20 to 25 cm (M 22.4).

530 This form is found in the Caucasus. Outside the USSR, in Asia Minor, in the western parts of its range, and possibly in the western parts of Iran.

2. Turkmenian bearded goat, *C. a. turcmenica* Zalkin, 1950. (The name *blythi* was applied to this form.)

In color and size this form is similar to the Caucasian form (*C. a. aegagrus*) but has slightly thinner and lighter horns.

Overall length of skull in adult males 250 to 279 mm (M 262.5) and in adult females 224 to 234 mm (M 227.5). Circumference of horns of adult males at base 18 to 23 cm (M 19.8).

This form is found in the Kopet-Dag and Gyaz'-Gyadyk (in Badkhiz). Outside the USSR it occurs in the Turkmen-Khorasan mountains in Iran.

The bearded goat of Turkmenia until recently was assigned to the form *blythi* Hume, described from Sind (Flerov, 1932). This form, it is usually thought, is somewhat smaller than the nominal form and with thinner horns. An even smaller size is acknowledged for Turkmenian animals.

As can be seen from the diagnostic features given above (Tsalkin, 1950), the smaller size of Turkmenian goat is not definitive, and only its slightly thinner horns can be considered its chief characteristic. It should be pointed out that this feature is also characteristic of the form *blythi* as well as of *neglecta*, described from Seistan. Nor are

Sind and Baluchistan goats, as can be seen from more recent data, as small as usually assumed. Their height at the shoulders is about 93 cm. The length of horns often reaches 100 cm (record, 130 cm along the curvature). The circumference of horns at the base is actually small, about 18 cm (Prater, 1947). This figure is less than that of the nominal form but very close to the diagnostic measurement for the form *turcmenica.* All this points out that the form *turcmenica* is very poorly characterized and probably occupies an intermediate position between *aegagrus* and *blythi* and *neglecta,* and most probably should be relegated to synonomy. Geographic data also support this view. It is possible, however, that it exhibits some color differences from the southern forms. The name *turcmenica* is tentatively retained here, therefore, until the characteristics of *C. a. blythi* and *C. a. neglecta* are better understood.

Outside the Soviet Union the form *C. a. blythi* Hume, 1875 is known from Sind, Baluchistan, and southeastern Iran (the precise boundaries of its range are not known). The name *C. a. neglecta* should probably be placed among the synonyms of this form. Some workers have described the following forms: *C. a. dorcas* Reich., 1888 from Yioura Island, north of Euboea in the northern Sporades; *C. a. pictus* Erh., 1858 from Andimilos Island in the Cyclades; and *C. a. cretica* Schinz, 1838 from Crete. The animals from these Aegean Sea Islands (if these forms have not yet become extinct) have no doubt hybridized with domestic goats; probably so have the Cretan forms. In the latest reviews none of these three western forms is usually acknowledged. While this is correct with respect to the forms of the Aegean Sea Islands, it may be unjustified for the Cretan. (V.H.)

Biology

Population. In the Soviet Union the maximum number of bearded (bezoar) goats survived in the western part of Dagestan: in the upper reaches of the Andii and Avar Kois and in the Bogos range separating them (Heptner and Formozov, 1941). There are significantly smaller number of goats in Georgia (more common in Akhmetov region—former Tushetiya; very rare in Svanetiya), Armenia, but more in Azerbaidzhan. In Armenia, in the Urts range (known to be comparatively rich in goats), an average of 37 animals were counted per 1,000 hectares of range inhabited by them (Dal', 1951).[158] In Turkmenia the numbers of goats is more than in the Caucasus; at places their population density is very high, sufficient to permit 531 some hunting. This is true of some places in Kopet-Dag, mainly the middle and eastern regions, and of the montane Gyaz'-Gyadyk area lying on the right bank of the upper Tedzhen in Badkhiz. The Bol'shoi Balkhan range was well populated by these goats until recently (V.G. Heptner). In the central regions of Kopet-Dag (Laptev, 1936) in 1934, in an area of about 1,500 km^2 about 1,000 to 1,500 bearded goats were estimated, or an average of 7 to 10 animals per 1,000 hectares of mountain slopes. For the Soviet Union as a whole the population of bearded goats may be placed at several thousand; in most regions the population is much less than what it was 50 to 100 years ago.

---

[158] This figure is obviously an exaggeration (Copy Editor) [L.P. Petrovskaya; see colophon, Russian original].

Habitat. The habitat of bearded goats in different parts of their range varies significantly. In Dagestan and Georgia goats are most often found in the middle mountain levels at a height of 1,200 to 2,200 m, where they were intensely persecuted in the recent past. Goats may be seen close to glaciers and the permanent snow line. Bearded goats prefer steep and rocky slopes (but do not avoid relatively gentle ones), especially if they alternate with sections covered with forest or shrubs. This occasioned one of the Dagestan names for bearded goats, i.e., "forest goat" (Heptner and Formozov, 1941). Most tur in these same regions are confined to much higher levels than bearded goats, and at places where tur are found in the forest belt of mountains they largely tend to gather on the forest-free slopes, (Dinnik, 1910; and others). In the mountains of Armenia, which have been intensely denuded by man, bearded goats often occur in open mountain-steppe meadows but, even in this part of their range, they exhibit a noticeable preference for mountains in which there are pockets of shrubs among boulders and rock slides. In Armenia goats inhabit the mountain belt from 550 to 3,200 m,[159] more often at heights of 1,500 to 2,500 m (Dal', 1954).

In the Kopet-Dag bearded goats quite often live on mountain slopes which are almost, or quite, devoid of woody vegetation, but they are usually scarce at places where juniper and other shrubs have been felled. Females are confined to much lower slopes than adult males, which are also found in rocky and less accessible sections of the mountains (Ognev and Heptner, 1929; Morits, 1930). In the Gyaz'-Gyadyk (Badkhiz), with a maximum height of 1,100 m, goats live at low elevations and are sighted along shallow and less accessible gorges. Compared to mountain sheep, bearded goats here, as also

[159] In Ararat, outside the Soviet Union, goats were encountered in summer at a height of 4,200 m (Radde, 1899).

in other parts of the geographic range, are more stenotopic (Heptner, 1956). In the Bol'shoi Balkhan range, i.e., the northern boundary of the geographic range in middle Asia, bearded goats are seen even in the foothills, at a height of 100 to 200 m above the Caspian Sea, under semidesert conditions (Laptev, 1934). At Kubadag near Krasnovodsk they were sighted in winter at sea level (Radde, 1889).

Food. Information about the diet of goats is limited mainly to Armenia (Dal', 1944, 1949, and 1951; and others). Goats relish twigs and leaves of various shrubs (hackberry, buckthorn, almond, honeysuckle, and wild cherry; in Kopet-Dag, they nibble juniper) and not less than 40 varieties of herbaceous plants, mainly grasses, lucerne, prangos, *Hippomaratrum crispum,* hedge nettle, winterfat, onion *Allium,* starch hyacinth *Muscaris caucasicum,* and others (Dal', 1944, 1949, and 1951).

In May in the Urts range it was noticed that goats licked at the same place (usually called solonetzes) on limestone outcrops and clay containing a large amount of sodium and calcium salts (Dal', 1951).

Home range. The dimensions of the home range are not known. In Armenia goats lead a more settled way of life than mountain sheep (Sarkisov, 1944). This settled mode of life has also been observed in Gyaz' Gyadyk (Heptner, 1956).

Daily activity and behavior. In the Armenian mountains in the warm period of the year bearded goats graze mainly in the morning (up to 9:00 to 10:00 a.m.) and in the evening (from 4:00 to 6:00 p.m.). Even in early night hours they may be seen in pastures. The animals spend much of the day in their bed under cover of overhanging
532 rocks, in the shadow of shrubs or trees, sometimes hiding in caves. Foraging areas, water holes, and beds are often 0.5 to 1.0 km apart (Dal', 1951; and others). Bezoar goats of the Kopet-Dag lead a similar mode of life; in the event of a drop in barometric pressure and thunderstorms goats descend to lower levels (Morits, 1930).

Bearded goats scale rocks almost as skillfully as tur. In the former the senses of smell, hearing, and vision are well developed. At places where bearded goats and tur are sympatric as in Dagestan, the former, according to Dinnik (1910), were characterized by a lesser degree of caution; they came closer to human dwellings and it was easier to approach them.

Adult males and females live singly for much of the year or form groups of 3 to 7 or sometimes even up to 20 to 30 animals. In the past, when bearded goats were numerous, they were encountered in herds of 40 or even 90 animals (Dinnik, 1910). Large herds are more often encountered in autumn and winter but vary in composition. While grazing or when fleeing, these herds readily split into smaller groups.

Seasonal migrations and transgressions. In most regions in winter goats descend to a lower level on the slopes, completely abandoning higher meadows. Rocky mountains covered with sparse trees and shrubs serve as wintering sites. In Dagestan tur do not descend to levels as low as bearded goats (Razevig, 1904). In the Kopet-Dag downward migrations occur immediately after the formation of a significant snow layer and, as soon as it thaws, goats return to higher levels (Morits, 1930). In the Gyaz'-Gyadyk there are no seasonal migrations of goats (Heptner, 1956).

Reproduction. Rut in goats commences from the middle to the end of November and continues for two weeks, terminating in the first half of December. In the period of rut males and females live together and serious fights are quite common among adult males (Dinnik, 1910; Morits, 1930). Parturition in Dagestan occurs usually at the end of May to early June, roughly at the same time as in tur (Dinnik, 1910). In Armenia and Turkmenia, for the most part, it occurs in the latter half of May (Dal', 1944 and 1951; Heptner, 1956). In southern parts of the range of bearded goats in the USSR, parturition in some years commences even in early May and probably even at the end of April. The female bears one or two kids, in rare cases three. She secludes herself before parturition in highly inaccessible places. Some females remain barren.

Goats evidently become sexually mature in their second year but many females produce kids only in their third year. Young males cannot successfully challenge more powerful older males and probably cannot mate before their third or fourth year.

Growth, development, and molt. The first two or three days after birth kids remain in one place and remain immobile in the event of danger. Later they follow their mother everywhere. Kids become independent of their mother at the age of seven to twelve months, but sometimes only by the autumn of the second year.

The nature of horn development is essentially similar to that of Siberian ibex, which have been studied in great detail (Tsalkin, 1950). In Armenia adult females more often weigh 26 to 30 kg and males 35 to 38 kg (Dal', 1951) but these do not represent the maximum. In the Kopet-Dag where the much smaller form of bearded goat lives, compared to the Caucasian goat, the weight of males may exceed 55 kg (Morits, 1930). According to Vereshchagin (1947) the weight of adult male bearded goats is comparable to corresponding figures for tur.

The shedding of winter hair in summer occurs very gradually—from April to the end of June (in Turkmenia, it is possibly earlier; even in May in most animals). The last to molt are old males and females, in which winter hair remains for the longest period on the flanks (Morits, 1930; Dal', 1944 and 1949). The period of growth of winter hair has not been studied.

The longevity of these goats exceeds 10 to 12 years.

Enemies, diseases, parasites, mortality, competitors, and population dynamics. Lynx, wolf, and leopard are among the enemies of goats, while golden eagle and evidently the manual [Pallas' cat] attack kids.

533 In summer goats are severely troubled by gadfly, skin mite *Hypoderma aegagri,* horsefly, and other dipterans. In the Kopet-Dag they are infected by juveniles of skin mites more intensely than wild sheep (Tsalkin, 1948). Instances are known of goat mortality due to necrobacillosis and other diseases which are common among domestic animals. In Armenia 22 species of helminths have been detected among goats (26 animals examined). Of these helminths, 20 species are common to domestic sheep and goats. The nematode *Protostrongylus davitiani* was found in 92% of the animals studied (Grigoryan, 1949).

At present, the main competitors of bearded goats are domestic animals, especially domestic goats and sheep which consume predominantly the same species of plants as bearded goats do. Mountain sheep live on more gentle slopes and are not usually found in the habitats of bearded goats (Sarkisov, 1944).

The population reduction in bearded goats is due not only to direct persecution by man but also to destruction of trees and shrubs in the mountains, thereby destroying goat habitat (Dinnik, 1910; Morits, 1930; and others).

The population composition is almost unstudied. In May, 1950 in the Urts range (Armenia) before the commencement of parturition, the population of bearded goats comprised 36.5% animals aged one to two years and 63.5% older than two years, of nearly equal numbers of males and females (Dal', 1951).

Field characteristics. Bearded goats differ from tur not only in their much lighter body build and short and relatively thick legs, but also in the greater amount of blackish-brown or brownish-chestnut pigment in their coat. These colors are also seen in the line along the vertebral ridge, the head, beard, front of chest, legs, tail, etc. The horns of males are crescent-shaped, laterally compressed, and reach 50 to 60 cm or sometimes even 130 cm in length; their anterior edge forms a sharp ridge with wide-set knobs (usually no more than seven to nine knobs). In the majority of females the horns are no longer than 15 cm (Dinnik, 1910; and others).

Bearded goats very rarely vocalize; their voice is similar to that of domestic goats, but harsher. Yearlings can jump across 2.0 m while adults can span a distance slightly greater than 3.0 m (Dal', 1951; and others). At places of permanent goat residence one commonly sees narrow trails (often along rock ledges), feces, tufts of light-colored winter hair on bushes, bushes with bark totally removed by horns, and so on. (A.N.)

Economic Importance

Bearded goats were mainly hunted for their meat and hide; horns were used as wall decorations. In the Middle Ages in Europe and Asia bezoars were greatly valued as possessing magical curative properties (whence one of the names of these goats); they are mineralized concretions of food and hair that accrete around nuts, stones, and so on. These hair balls were not used in the Caucasus, but were quite often used in Russia in the seventeenth century (see p. 756).

No data are available on the extent of hunting in the past. One hunter in a hunting party in the central Kopet-Dag in the winter of 1940/41 purportedly bagged 362 bearded goats and in 1941/42, 374 goats (Tsalkin, 1948). Bearded goats are hunted with both rifled and smoothbore firearms. Hunting is from ambush, by stalking or chasing, often with the help of hounds. In Dagestan a few decades ago goats were caught in traps (Dinnik, 1910). Nowadays hunting of bearded goats is prohibited throughout the USSR.

Bearded goats are the ancestors of domestic goats. In captivity they interbreed with domestic goats, Siberian ibex, and tur, yielding fertile offspring, which are sometimes larger in size than the parent forms. In the Negram mountains (Pfizenmayer, 1915) and in Dagestan (Heptner and Formozov, 1941) animals similar in color to bearded goats are quite often seen among domestic goats. Hybridization in 534 nature of goats with tur has been observed near Borzhomi, where tur were acclimatized, and also in the upper reaches of the Aragva (Pfizenmayer, 1915). Hybridization in nature of bearded and alpine ibex has also been noted in Czechoslovakia, where both species were acclimatized.

The institution of special preserves, primarily in Dagestan and Armenia, would be useful for the conservation of bearded goats.

In Russian zoological gardens bearded goats do not thrive as well as other mountain goats, evidently due to the inadequate study of their biology (A.N.).

17. SIBERIAN MOUNTAIN OR ROCK GOAT[160] [Siberian ibex]

Capra (Capra) sibirica Pallas, 1776[161]

1776. *Ibex sibiricus.* Pallas. *Spicil. Zool.*, vol. 11, p. 52. Munku-Sardyk, northern slope of the Sayan.[161]

1838. *Capra pallasii.* Schinz. *N. Denkschr. Schweiz. Ges. Naturwiss.* Substitute for *sibiricus* Pallas.

1842. *Capra sakeen.* Blyth. *J. Asiat. Soc. Bengal,* vol. 11, p. 283. Tibetan slopes of the Himalayas.

1900. *Capra sibirica lydekkeri.* Rotschild. *Novit. Zoolog.*, vol. 7, p. 277. Katun range, Altai ("Katutai range in Pri-Irtysh Altai").

1902. *Capra altaica.* Noak. *Zool. Anz.*, vol. 25, p. 623. "Pri-Irtysh Altai."

1902 *Capra fasciata.* Noak. *Zool. Anz.*, vol. 25, p. 623. Neighborhood of Lake Telets, Altai.

1902. *Capra alaiana.* Noak. *Zool. Anz.*, vol. 25, p. 624. "Most probably Alai mountains." More precisely, central Alai range.[162]

1905. *Capra sibirica lorenzi.* Satunin. *Priroda i okhota* [Nature and

---

[160] This name is largely artificial and simply a translation of the Latin; however, it is widely used.

Recently, for some reason, this species has sometimes been labeled the Siberian "capricorn" or simply "capricorn". This makes no sense whatsoever. This is not an animal with the horns of a goat but a true goat per se. For exactly the same reason the name "Siberian goat" has been altered to the quite unwieldy name "Central Asian goat," based on the fact that the species is more extensively distributed in Central Asia than in Siberia. This is a needless purism and furthermore lacks adequate geographic justification.

Russian hunters simply call the animal a goat or use local names of non-Russian origin—bun in the Altai, tek or teke in the Tien Shan, and others.

[161] In Soviet literature until recently the Siberian ibex was customarily identified as *sibirica* Meyer, 1794 based on the assumption that the name given by Pallas in the *Spicilegia—Capra alpium sibiricorum*—was not binomial. However, this name, actually unsuitable, was given in the second edition (1766), while the name given here, altogether appropriate, and used in western literature, was assigned in 1776 in the eleventh edition of the Spicilegia.

[162] The description of the form *alaiana* is based on a subadult live animal brought from Tashkent (not from a hide bought in Tashkent as reported by Tsalkin, 1950) and it is a "highly probable" ("höchst wahrscheinlich") that it came from the Alai range. This report (as also the entire description), is, of course, inadequate but with the Latin name sufficed for a precise identification of terra typica, at least in the manner done above. Quite recently it has been suggested (Tsalkin, 1950) that Saryk-Mogul, in the Trans-Alai mountain range, be considered the terra typica of this form. This is unacceptable not only for the reasons stated above (this site is the terra typica of the form *transalaina* and to designate it in the corrigenda as the terra typica of another form, described earlier, is illogical), but also because it lacks practical significance.

Hunting], vol. 5, p. 22, 320 versts south of Nizhneudinsk (Sayans).

1906. *Capra sibirica typica.* Lorenz. *Denkschr. K. Akad. Wiss. Wien,* vol. 80, p. 95. Tunkin alps, Sayans.

1906. *Capra sibirica almasyi.* Lorenz. *Denkschr. K. Akad. Wiss. Wien,* vol. 80, pp. 89 and 98. Aksu in the Tersk Alatau.

1906. *Capra sibirica transalaiana.* Lorenz. *Denkschr. K. Akad. Wiss, Wien,* vol. 80, pp. 90 and 103. Saryk-Mogul, southern slope of Trans-Alai range. 536

1906. *Capra sibirica merzbacheri.* Leisewitz. *Zool. Anz.,* vol. 29, p. 655. Western part of the Tien Shan. More precisely, the upper Great Naryn [River].[163]

1949. *Capra sibirica formosovi.* Zalkin. Tsalkin. *Byull. Mosk. Obshch. Isp. Prir. Otd. Biol.,* vol. 4, no. 2, p. 20. Aleksandrov range, Kyyamattu gorge 26 km southwest of Novo-Dmitriev station. (V.H.)

Diagnosis

Large-sized goat. Horns long, curved like a scimitar in a single plane, with broad and flat anterior surface, and transverse ridge-shaped knobs. Horns triangular in cross section. Distinct dark band occurs along spine. Beard fairly heavy. Tress of long hair absent on neck and chest. (V.H.)

Description

The Siberian ibex is a large animal, in fact the largest of all the species of the genus, with a stout body standing on low, fairly thick, firm legs, with a large and deep rib cage, slightly higher at the sacrum than at the withers. Neck relatively short and strong; head proportionate with quite a broad forehead. Beard broad, thick, and long. Tail short, flat, and bare ventrally.

Horns of the Siberian goat are very large, massive, and curve

---

[163] The author in describing this form from the western Tien Shan had in view the western half of the mountain range as a whole, i.e., mainly that part which falls within the Soviet Union.

The above precise location is based on a more detailed reference to the distribution of this form given in the text of the original description: ". . . evidently from the peak of Nikolai Mikhailovich in the west across the Sary-dzhas and its lateral valleys up to the region of the upper reaches of the Great Naryn" (Leisewitz, 1906, p. 355). Nikolai Mikhailovich peak rises to a height of over 6,000 m and is located in China not far from the Russian border, east-northeast of Khan-Tengri.

backward in the shape of a scimitar. They are larger than those of all other Russian goats, and in general larger than those of all other species of the genus. Horns have a broad, smooth anterior surface and sharp inner and outer ridges.[164] Lateral margin of horns turned back and posterior ridges slightly rounded. On the whole in transverse section horn triangular in profile with a smooth posterior ridge. Sharp, prominent knobs in the form of transverse ribs or ridges present on anterior surface. Knobs absent at very tip of horn but faintly seen proximal to it ([growth] segment of second year). Knobs sharp in all other segments and usually two, rarely one or three, ridges occur in each.

Horns usually curved in a single plane and set quite steeply on the skull; they diverge from the base at a small angle, usually 45° or less. Keratin black.

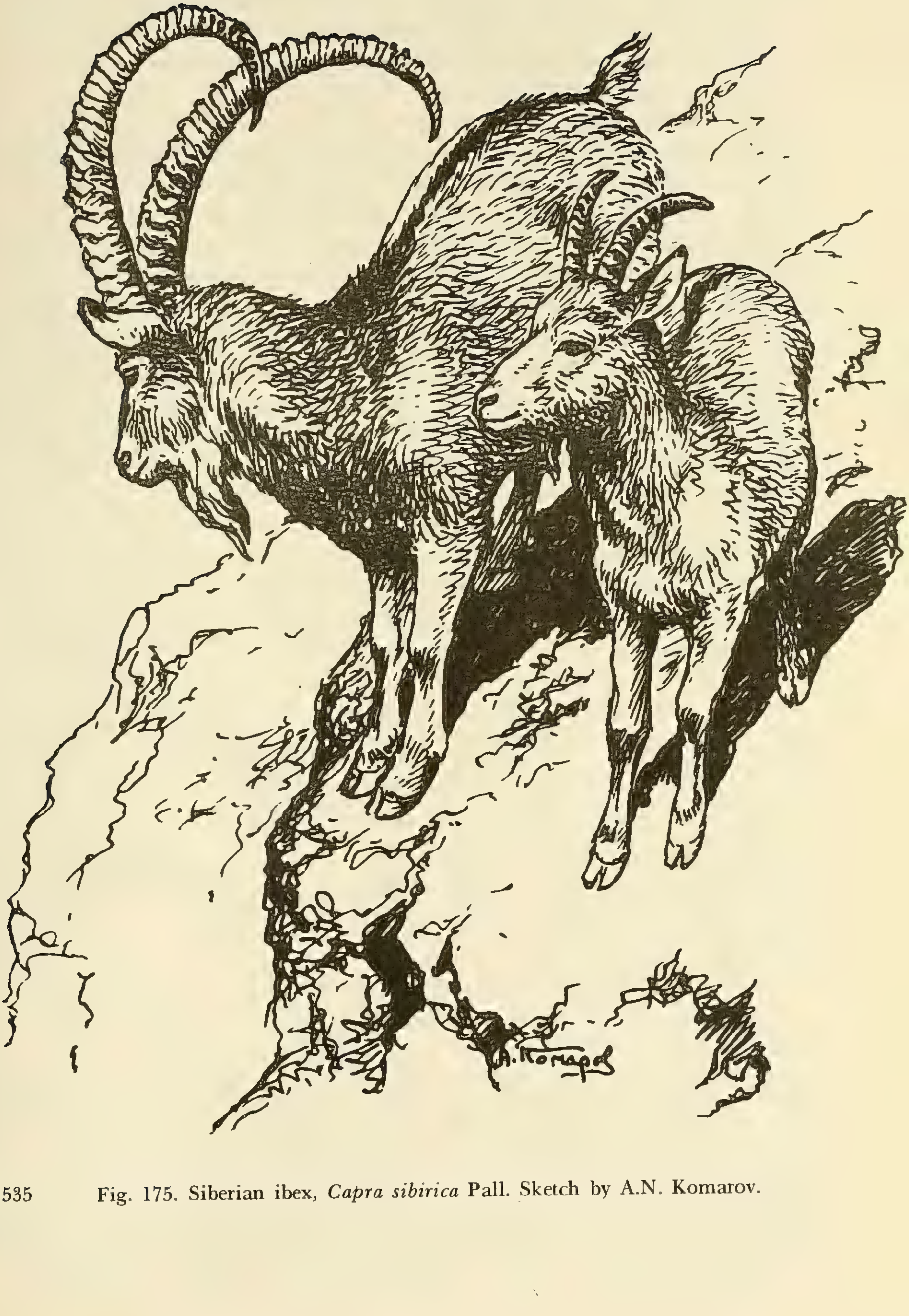
The horns described above are highly characteristic of Siberian goats and their main structural features are preserved in all parts of the range. However, some aspects of horn development exhibit high individual variability. For example, the curvature of the horn may be weak and the horn almost straight, at least much of it or, contrarily, the curvature may extend for half or even more of the length of the horn. Horns may be set almost parallel to each other throughout their length or, on the other hand, be highly divergent. Horn bulk (ratio of thickness to length) is also variable; some horns are thin and long and others very short and thick. Not only the number,
537 but also the size and form of the knobs on the anterior surface of the horn are variable. Sometimes they are very rough and large, sometimes faint, and exceptionally are absent altogether, with only gentle protuberances present at the corresponding places.

Horns are always present in females but much smaller than in males; their length is less than one-third that of males (not longer than 37 to 38 cm). They are very thin and weak (horn circumference at base not more than 13 or 14 cm), elliptical in cross section, knobs not formed on flat anterior surface, the surface being rugose. The small female horns curve very gently and diverge sideways slightly.

Coloration in the Siberian ibex is highly variable. Sex-related and seasonal variation, often age-related variations also, are distinct and individual variability prominent. Geographic variation in coloration is likewise significant, much greater than among other goats.

---

[164] In other forms with a similar type horn (*C. ibex* and *C. nubiana*) the outer ridge of the anterior surface is less pronounced than the one on the inner surface. At least this is the case in the material available in the Zoological Museum of Moscow University.

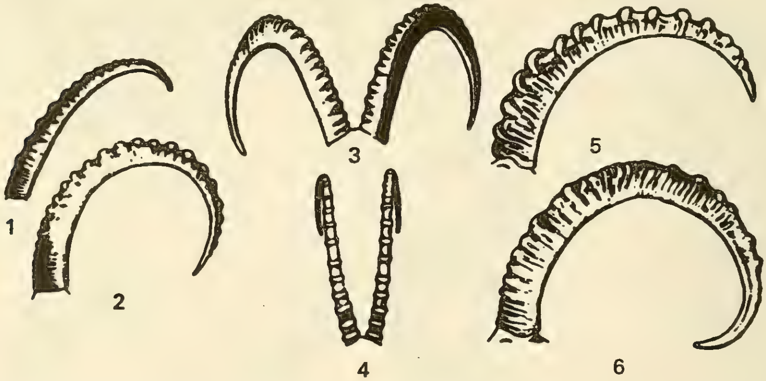


535 Fig. 175. Siberian ibex, *Capra sibirica* Pall. Sketch by A.N. Komarov.

Thus Siberian ibex from the northeastern part of the geographic range (the Sayans, Altai, and the mountain systems associated with them) are readily distinguished by coloration from ibex in the southern and southeastern parts (Tien Shan system, Pamir-Alai, and more southern mountains).

The winter coat of adult males of Altai-Sayan ibex is very light; "the back, flanks, and entire upper portion of the neck are a dirty or yellowish-white, forming the main background of the overall color of these animals. A fairly dark and vivid brownish-cinnamon band runs along the spine and continues onto the upper surface of the tail, where it appears even darker and more vivid, sometimes even cinnamon-black. Shoulders are also brownish-cinnamon of varying intensity. Quite often the dark coloration on the right and left shoulders continues as a single transverse field across the spine, isolating the light-colored field on top of the neck. The length and width of this dark band varies greatly. Sometimes it is totally absent, in which case the light coloration of the back and the upper portion of the neck merge into a single common field.

The dark coloration on the shoulders may extend down along the front of the limbs right up to the hooves, becoming increasingly vivid or turning dark cinnamon. The rear part of the forelimbs is very light, yellowish or dirty white. The degree of development of the light coloration in the rear part of the forelimbs is quite variable.



537 Fig. 176. Individual variations of horn structure in Siberian ibex, *Capra sibirica* Pall. Sketch by N.N. Kondakov mainly based on material of the Zoological Museum of Moscow University (from Tsalkin, 1950).

1 and 2—extreme forms of curvature of horns (specimens from Tien Shan); 3 and 4—position of the horns in relation to each other (sometimes tips slightly turned in; specimens from Pamir); 5 and 6—varying degrees of development of knobs on front surface of horns (specimens from Tien Shan).

Along the lower part of the flanks, from the shoulders to the thighs, 538 a dark band occurs, which varies greatly in coloration; sometimes it shades toward pale brown, sometimes bright cinnamon. The abdomen is much lighter, brownish or yellowish-gray, and the groins very light, a yellowish-white. The anterior portion of the thighs and lower sections of the hind limbs are generally the same color as the shoulders and forelimbs. The lower part of the neck and chest are a dark, brownish-cinnamon. The lighter upper part of the neck gradually darkens toward the head and becomes cinnamon-brown on the occiput, forehead, and on the cheek. In front of the eyes a dark cinnamon-brown band runs across the face, gradually lightening and extending onto the cinnamon-brown color of the nose" (Tsalkin, 1950).

Individual color variation in this species, a common feature throughout its range, is mainly exhibited in varying intensity of tone of the dark bands. Color ranges from a relatively dull cinnamon-brown to a vivid blackish-cinnamon. Evidently, some variations are due to fading of hair color toward spring. Sometimes the color contrast is weak because of darkening (graying) of white areas. Exceptionally, individuals are seen in which the light-colored areas are relatively dark (yellowish-gray) and the dark-colored areas light or even indistinguishable from the light-colored ones, giving the animals a uniform coloration.

In the summer coat "the general shade of color is grayish or cinnamon-brown. There are no traces of dark coloration on the shoulders, thighs, and chest, so characteristic of the winter coat. Hence the color becomes a uniform monotone. On the flanks the color gradually lightens and merges without demarcation into the dirty or yellowish-white shades in the region of the abdomen and groins. Along the midline of the back a narrow, dark-cinnamon colored stripe is usually seen. The intensity of dark coloration on the anterior surface of the limbs varies. Coloration of the head is similar to that of the trunk; as in the winter coat a dark transverse field occurs on the snout in front of the eyes. The tail and the beard are a dark cinnamon" (Tsalkin, 1950).

Sexual dimorphism is sharp. "In females the back, flanks, and upper part of the neck in the winter coat are grayish-brown with a cinnamon or chestnut tinge of varying intensity. Dark coloration on the shoulders, chest, and thighs is absent; they are the same color as the back and flanks. Dark areas on the flanks are absent and their color, lightening gradually, merges into the whitish abdomen and groins. Dark stripe on the midline of the back is absent or poorly visible. Tail dark cinnamon. Head coloration more intensely gray than that of trunk. Anterior surface of limbs darker but not very vivid.

"Coloration of adult females in summer is very similar to that of winter, differing only in a somewhat darker cinnamon-brown shade in summer.

"Coloration of juvenile males very similar to that of females (true of winter as well as summer coat). The characteristic color contrasts of the winter coat described above develop fully in adult males only in their fourth or fifth year" (Tsalkin, 1950).

The color of Tien Shan and Pamir-Alai ibex differs markedly from what has been described above. "In the winter coat the back and flanks of adult males are cinnamon-brown of varying intensity. On the back and sometimes even on the upper portion of the neck a fairly vivid light-colored spot occurs, varying highly in size and shade. Sometimes it is quite large, with a width of about 20 cm, and sometimes narrow. In individual cases it may consist of no more than odd white hairs on the back at the point corresponding in location to the light-colored spot in other animals, and relatively undistinguishable against the general background. Dark stripe on the midline of the back usually present and well developed. Outer surface of the tail cinnamon-brown. Flanks duller than the back and brownish. A very dark band occurs along the lower part of the flanks, separating the whitish color of the abdomen and the groins. Coloration of the shoulders and thighs similar to that of the flanks. 541 A distinct dark brown band occurs on the anterior surface of the forelimbs, which is lighter in the hind limbs. Head lighter in color than the flanks and somewhat grayish. Dark transverse band on the snout absent in front of the eyes. Beard brown" (Tsalkin, 1950).

Individual variability in coloration is likewise high in animals in these regions. The light-colored spot on the back is sometimes totally absent. Similarly, individuals with a fairly uniform light gray color have been described (Demin, 1947). Female goats in this group evidently do not exhibit a light-colored saddle-shaped part (Tsalkin, 1950).

The skull[165] of the Siberian ibex is similar to that of bearded goat in general form and in several other features. The former is characterized as follows. It is larger (see below), with bony horn cores in transverse section resembling an isosceles triangle with the fairly broad, slightly bulging base set anteriorly. The sharp anterior ridge is therefore absent. The bony core is invariably curved slightly backward in a single plane. Prominences on the frontal bones anterior to the base of the bony core are absent. The forehead is therefore almost flat and not concave.

---

[165] See Figs. 177, 178 and 179.

The posterior and anterior edges of the horn core are separated from the edge of the orbit by less than the diameter of the orbit. The part of the skull behind the horns is relatively large and represents 26 to 27% of the total skull length. The cranium is broad and the skull very broad in the region of the orbits; its width along the posterior walls of the orbits constitutes about 53% of the total skull length. The skull is sharply constricted immediately in front of the orbits. The nasals project forward more than in other species of goats; a perpendicular line drawn from the anterior end of the nasals to the surface of the palate lies at a distance from the anterior end of
542 the tooth row equal to or greater than the length of the first three teeth (premolars). This distance is about 10% of the total length of the skull. Mesopterygoid fossa wide. Mastoid processes relatively large and thick.[166]

Size of ibex is extremely variable, depending on age and sex, and weight also changes markedly, depending on the season and year, i.e., extent of fattening. Moreover, some geographic variations in size, although insignificant, are also seen.[167]

Length of body of adult (four years and older) males 130 to 165 cm and of females up to 135 or probably slightly more; height at withers in males 80 to 100 cm, on the average about 92 cm, but in large animals up to 105, or even 110 cm. Length of ears in males 14 to 16 cm (same in females), length of tail 10 to 18 cm, and chest circumference in males 92 to 125 cm and in females 74 to 89 cm.

Length of horns along the curvature often up to 100 cm in males but may even reach 135 to 140 cm. Known maximum 147 cm. Circumference of horns at base varies from 18 to 28 cm. Maximum length of horns in females 37 to 38 cm and circumference at base 13 to 14 cm, usually less.

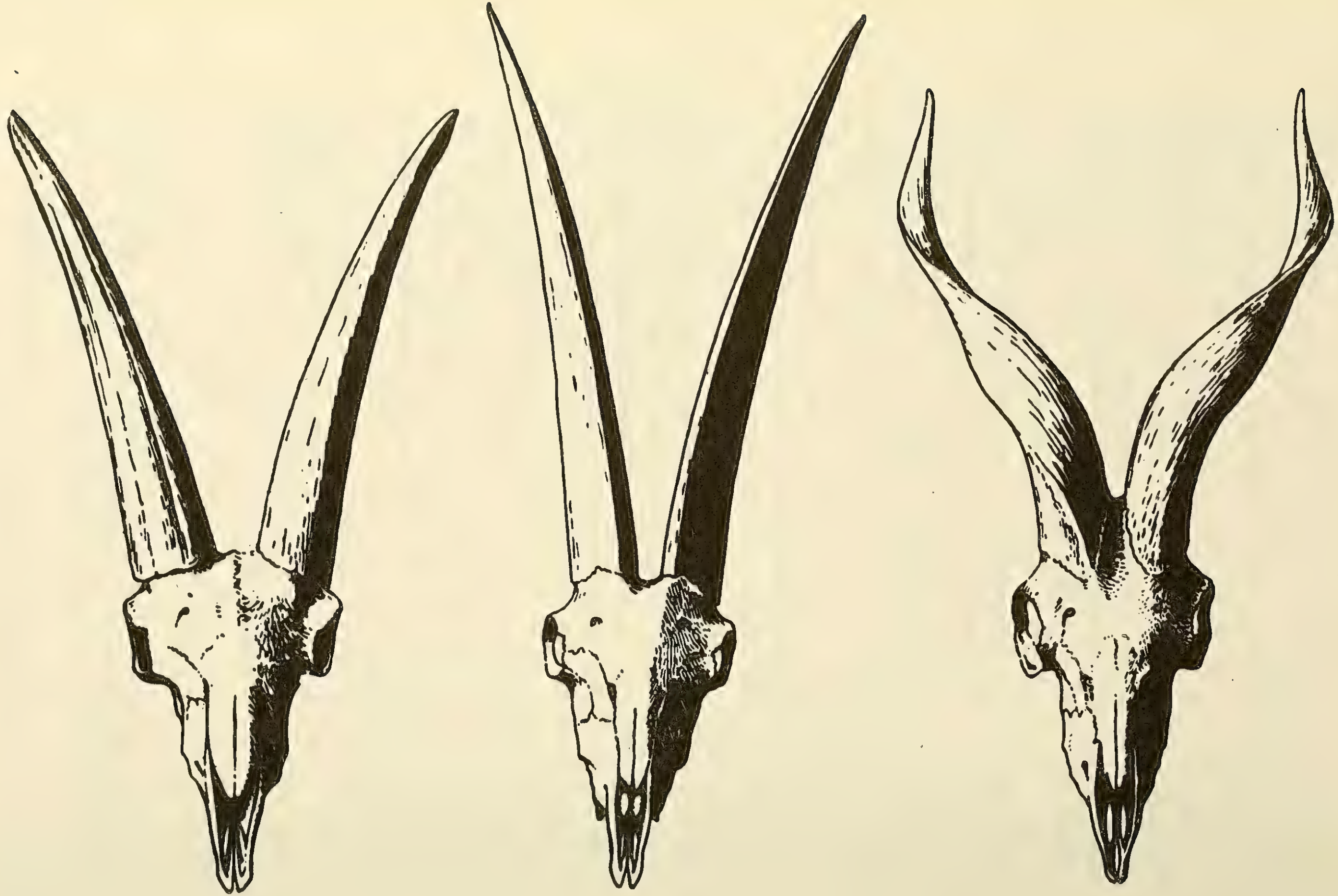
General weight[168] of well-fed males up to 100 kg or more, even 130 kg (Tien Shan). Maximum weight could probably be higher. Usual weight of males 80 to 100 kg. Weight of females up to 60 kg and rarely more; usually 30 to 40 kg. (V.H.)

---

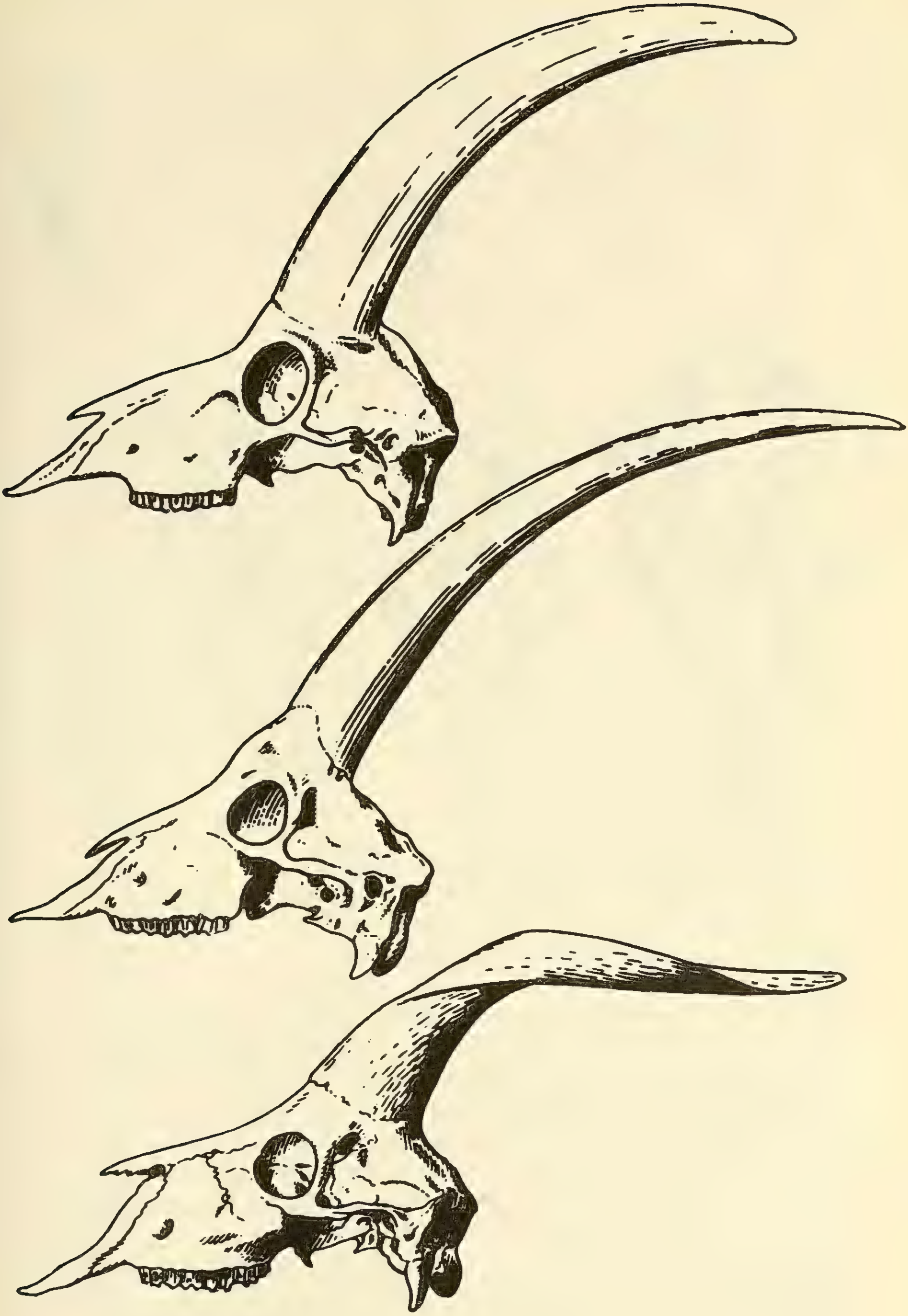
[166] Craniological data are from Tsalkin (1950). Some data from Gromova (1940) have also been incorporated.

[167] Information on the size and weight of goats is still scanty and not always accurate.

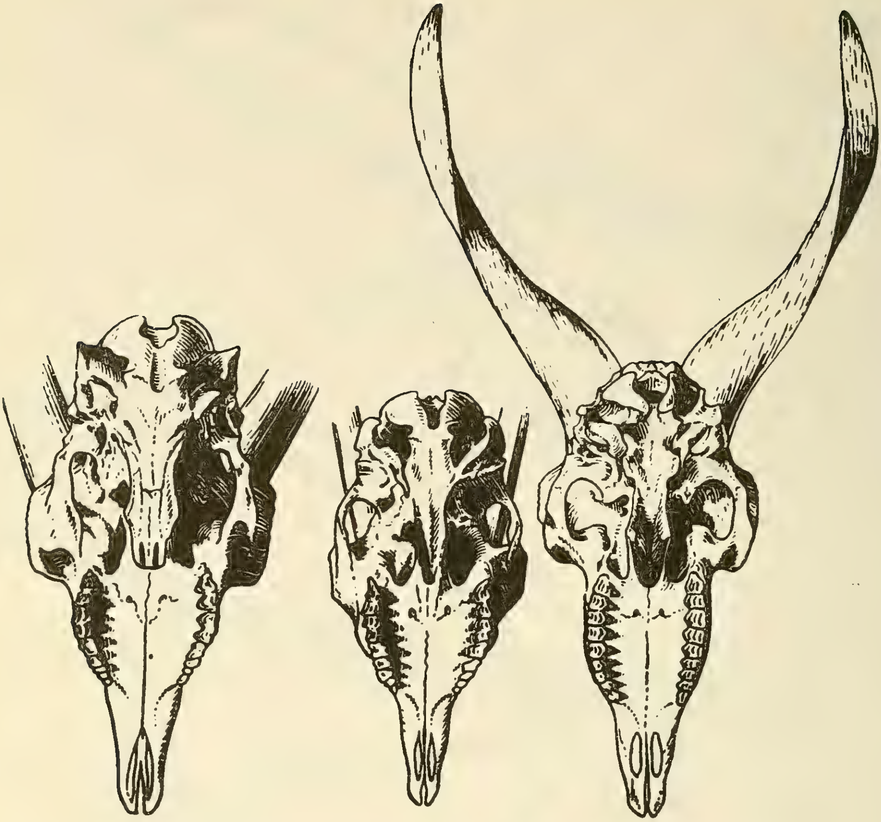
[168] According to Tsalkin, 1950; Egorov, 1955; and others. Some additional information on size is given in the section "Biology".



539 Fig. 177. Skulls (dorsal view) of male Siberian ibex, *Capra sibirica* Pall. (Pamir-Alai system); bearded goat, *Capra aegagrus* Erxl. (Kopet-Dag); and markhor, *Capra falconeri* Wagn. (Kugitangtau). Sketch by N.N. Kondakov based on material of the Zoological Museum of Moscow University (from Tsalkin, 1950).



540 Fig. 178. Skulls (lateral view) of three species of male mountain goats. Same specimens as depicted in Fig. 177. Sketch by N.N. Kondakov.



541 Fig. 179. Skulls (ventral view) of three species of male mountain goats. Same specimens as depicted in Figs. 177 and 178. Sketch by N.N. Kondakov.

Taxonomy

As mentioned above, the present state of our knowledge does not permit establishing with certainty the systematic position of individual forms of goats. It is, however, quite clear that it would be most rational to regard the Siberian ibex as an independent species. This view is supported also by zoogeographic data—its geographic range is separated from those of other forms with which it is usually linked (Alpine ibex *C. ibex*, Kuban tur *C. caucasica,* and Nubian goat *C. nubiana*), by the ranges of the bearded goat (*C. aegagrus*) and markhor (*C. falconeri*). The Siberian ibex often lives with the latter (markhor) in the same region (see below).

From a purely morphological viewpoint the species under description exhibits certain features in common with the Alpine ibex, but points of similarity, particularly in horn structure, are actually less than usually assumed (see above). Information is available (Tsalkin, 1955) to show that in craniological characteristics, among Russian forms the Siberian ibex exhibits greatest similarity to the Kuban tur (*C. caucasica*). On the whole, however, this species, like some others, obviously exhibits a combination of characteristics of the different forms. (V.H.)

Geographic Distribution

Siberian ibex are found in Mongolia, southern Siberia, Middle Asia, Afghanistan, northwest India, the western margins of Tibet, and northwestern China.

Geographic Range in the Soviet Union

The range in the Soviet Union represents a fairly significant part of the range of the species, i.e., the northern edge of its northern and northwestern parts. It covers a very small part of the Soviet Union in the eastern part of Middle Asia and in the extreme south of Siberia. Features of the range within the Soviet Union are extremely complex because of the pattern of mountain ranges; the geographic range comprises several individual sections, sometimes continuous with each other outside the Soviet Union.

Within the USSR there are two main, fairly independent, areas of occurrence of goats—southern Siberian and Middle Asian.

In the east the southern Siberian part of the range occupies Tunkin mountains (Dorogostroiskii, 1922; Favorskii, 1936) but does not
543 extend farther to the east or northeast.[169] In the northwest the range includes the Kitoi and Okin ranges and the entire montane region of the Oka, the Udin range, and the region of the source and upper reaches of the Uda River. In the Uda basin ibex are distributed up to the confluence of the Kara-Buren' and Uda rivers (Favorskii, 1936). The region where the headwaters of the basins of the Uda (Angara basin) and Kazyr (Tuba basin of the upper Yenisey) approach one another represents the northernmost point of ibex habitation. At least in the period under review the range did not extend farther to the northwest, along the eastern Sayan system (Kyzyl-Kyzyr range,

---

[169] Ibex evidently did not extend even in the middle of the eighteenth century east of the Sayans (Pallas, 1811). References to the occurrence of ibex at Lake Oron in the Vitim basin to the northeast of the northern extremity of Baikal (Favorskii, 1936) are positively erroneous.

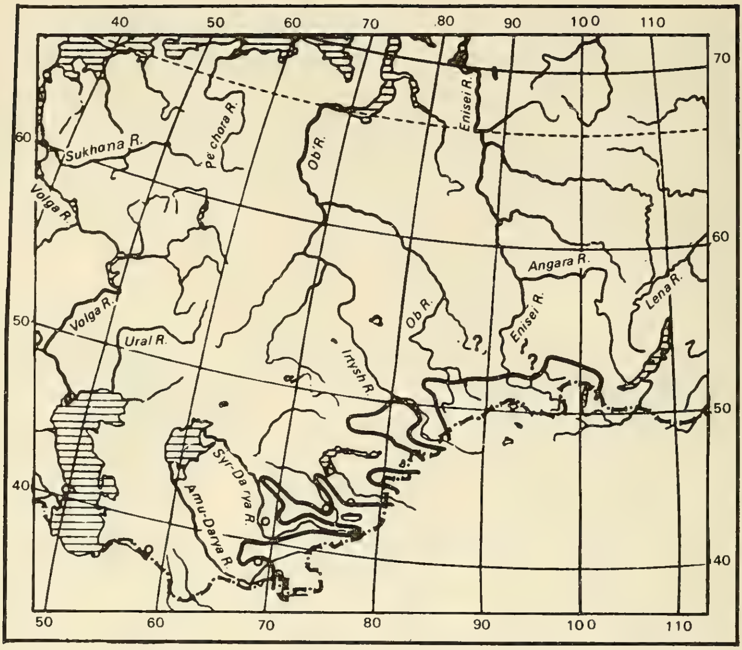

40
50
60
70
80
90
100
110
70
60
50
40
Sukhona R.
Pe chora R.
Ob R.
Enisei R.
Volga R.
Angara R.
Lena R.
Volga R.
Ural R.
Ob R.
?
Enisei R.
?
Irtysh R.
Syr-Da rya R.
Amu-Darya R.
50
60
70
80
90
100
110

Fig. 180. Reconstructed range of Siberian ibex, *Capra sibirica* Pall., in the Soviet Union. V.G. Heptner.

Kan, and Man Belogor'e [Snow Mountains]), i.e., toward Krasnoyarsk.[170]

The outline of the range of ibex is not clearly known to the southwest of the northernmost area of occurrence referred to above. They possibly occurred throughout this part of western Sayan to the Yenisey, i.e., in the Ergak-Torgak-Taiga range and farther southwest. However, there is no positive information about this. On the contrary, some references declare the absence of ibex in the region to the east of the meridian of Verkhne-Usinsk (Solov'ev, 1920) and along the rivers Kyzyr, Kazyr, and Amil (tributaries of the Tuba entering the Yenisey below Minusinsk), partly flowing from the above mountains (Zalesskii, 1934). The range covers the section of western Sayan directly adjoining the Yenisey from the east (Aradan range; V.H.) where the right tributary of the Yenisey, the Kazyr-Suk River, forms the northern boundary of the geographic range (Solov'ev, 1920).

Farther west, along the left bank of the Yenisey, the Sayan moun-

---

[170] Goats inhabited Krasnoyarsk and the region slightly above it [upstream] (left bank of the Yenisey) in the Paleolithic period (Gromov, 1948).

tains lie within the range. In the east of this montane area the range in the north covers the basin of the Dzhebash River (right tributary of the Abakan) and the Dzhebash range, continuing toward the Yenisey at the mouth of the Kantegir. Farther west the upper reaches of the
544 Ona and Malyi Abakan are included in the range (Zalesskii, 1934; Skalon, 1929 and 1936). The range also covers the region of the upper reaches of the Bol'shoi Abakan and the upland between it and Lake Telets; i.e., the southernmost extremity of the Abakan range and the entire meridianal Shapshal'sk (Chapchal) range up to the Soviet boundary (V.G. Heptner).

The above description outlines the Sayan part of the Altai-Sayan region of occurrence of ibex.

Our knowledge of the distribution of this species south of the above mountain system is poor indeed. In the extreme east, in the region of the Oka, it reaches up to the state boundary in particular, at Munky-Sardyk. In the west the range evidently covers the whole of the Tannu-Ol range (Yanushevich, 1952). The species probably also occurs in Sangilen in the extreme southeast of the Tuva district but there is no information about this. Similarly, the distribution is not clearly known throughout the Tuva district to the south of the above-mentioned northern mountains.

The absence at present of Siberian ibex in that portion of the western Sayan between the meridian of the Verkhne-Usin and the source of the Uda is evidently based on its extermination, probably in the last century. In much of the Abakan range (apart from the extreme south as noted above) ibex are not present. They are also absent (and were also absent in the period under review) in the Kuznetsk Alatau. At the same time, based on general zoogeographic and ecological considerations, it may be assumed that in the past (nevertheless in our era) they probably did live there. Thus the range evidently extended to the region of Krasnoyarsk not only from the east but also from the west, and the range in this territory was considerably larger than at present.

The Altai part of the range of the Siberian ibex encompasses almost the whole of the southern Altai to the state border. The northern boundary of the range in the eastern part of the Altai runs from the midcourse of the Chemal (right tributary of the Katun; Zelesskii, 1934), through Lake Telets (its northern part; Dmitriev, 1938) to the upper reaches of the Bol'shoi Abakan (V.G. Heptner). Farther west the northern boundary of the range encompasses Semin range (divide between the Katun and its left tributary, the Sema, at least the southern part), the Terektin range, Tigeretsko-Korgonskii mountains,[171] Kholzun and Listvyag ranges, the Belukha mountain massif, and the upper reaches of the Bukhtarma. The range also includes the Narym, Sarymsakty, Kurchum, and southern Altai. The range boundary proceeds to the state boundary in the region east of Lake Markakol'.

The Altai area of occurrence of Siberian ibex forms a continuous unit with the Sayans, with which it is confluent directly through the Abakan range and Shapshal.

Inside the boundary outlined above the distribution of the ibex is extremely uneven; it is found in isolated sections along individual mountains. These sections are often severely isolated (up to 100 km) from each other (Fig. 181). Such a dispersion is the result of not only geographic conditions and the attraction of the animal to steep slopes and rocks, often to the mountain tops, but mostly destruction and crowding caused by man.

The boundaries of the reconstructed range outlined above do not wholly represent its condition in the middle of the twentieth century. Ibex were already absent at a series of places along the periphery. Thus they are apparently not seen in Tigeretsk mountains, their occurrence being restricted to the interior sections of the Terektin; they are also absent in the Semin range and along the Chemal; at Lake Telets the range shifted significantly southward and the boundary runs along its southern extremity.[172]

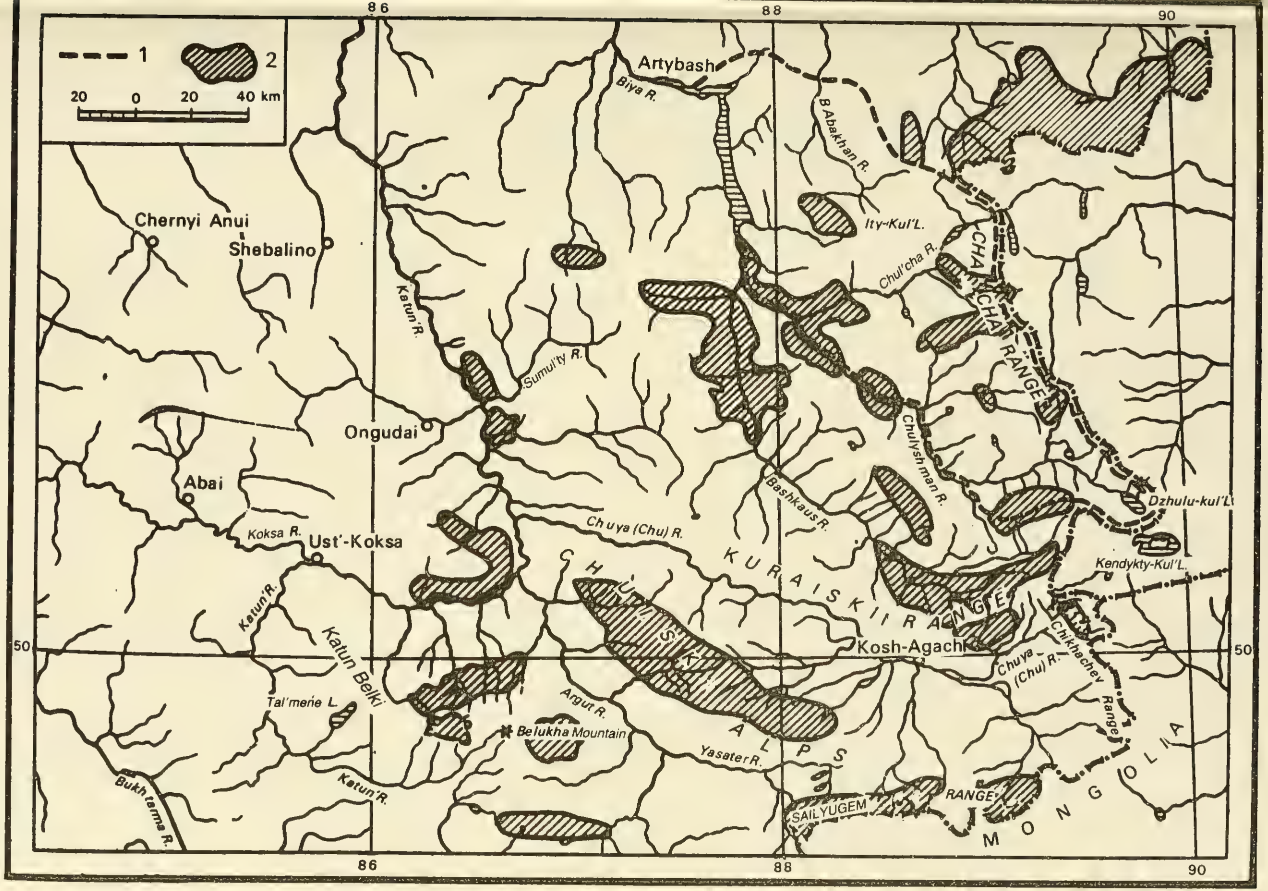
546 There is no doubt that in the remote past, for which we have no information, ibex were distributed in the Altai (as in the Sayan region) more extensively and occurred beyond the boundaries of the reconstructed range outlined above. There is reason enough to believe that the animals lived in the Ul'bin range, Ivanov gorges, Ubinsk mountains, and in Bashelak range (west of Shebalino), and probably the area of their distribution was broader. Had the animals not been persecuted they could have survived under suitable habitat conditions (steep slopes and rocks) even at very low altitudes.[173]

---

[171] The reference to occurrence along the Ine (Razorenova, 1939) pertains, however, not to the Ine River in the Charysh basin flowing from the Tigeretsk range, but to the Ine at the mouth of the Koksa on the Chuya.

[172] The geographic range in the Altai is based on data from Dmitriev, 1938; Razorenova, 1939; Zalesskii, 1934; V.N. Skalon, 1929 and 1936; Kolosov, 1939; Nasimovich, 1949; Antipin, 1941; E. Strautman, 1953; Turkin and Satunin, 1902; Kashchenko, 1902; Kuznetsov, 1948; and others and on original data of V.G. Heptner.

[173] In northern Afghanistan (Afghan Badkhiz) Siberian ibex live (or lived) in the rocky and even argillaceous outcrops rising above the surrounding area by only several hundred feet but with steep precipices and rocks. In moving from one outcrop to another the animals cross significant areas of plains (Thomas, 1889; Heptner, 1956).


1
2
20
0
20
40 km
86
88
90
50
Artybash
Biya R.
B Abakhan R.
Ity-Kul'L.
Chul'cha R.
CHA
CHA
RANGE
Chernyi Anui
Shebalino
Katun'R.
Sumul'ty R.
Ongudai
Abai
Koksa R.
Ust'-Koksa
Katun'R.
Katun Belki
Tal'menie L.
Chulyshman R.
Bashkaus R.
Chuya (Chu) R.
KURAISKII RANGE
CHUISKIE ALPS
Kosh-Agach
Dzhulu-kul'L.
Kendykty-Kul'L.
Chikhachev Range
Chuya (Chu) R.
Argut R.
Belukha Mountain
Yasater R.
Katun'R.
Bukhtarma R.
SAILYUGEM RANGE
MONGOLIA

545 Fig. 181. Distribution of Siberian ibex. *Capra sibirica* Pall., in the Altai (from Dmitriev, 1938; with modifications).

1—boundary of Altai preserve; 2—areas of occurrence of ibex.

Occurrence on the tops of high mountains, characteristic of ibex at present, is largely the result of direct persecution and displacement of the animals.

The Middle Asian part of the range includes the mountains of the Tien Shan and Pamir-Alai system and some highlands of eastern (Pri-Irtysh) Kazakhstan.

Ibex occupy the Kalbin Altai, some highlands on the left bank of the Irtysh associated with it (Del'begeteiskii mountains), and the area in the northwest to the Semipalatinsk region and in particular to Kokon' mountain, which lies southwest of the city (Selevin, 1925 and 1937). The range extended even farther west and northwest, evidently into the southern parts of the Karkaralinsk mountains ("Ortau mountains"; Von Hern, 1891). These represent the northernmost points of the range.

To the south the range includes the Tarbagatai and Saur (Sedel'nikov and Borodin, 1903; E. Strautman, 1953) and the whole of the Dzhungarsk Alatau (in particular the Kopal region, along the Kora, the Kugalin range, Matai and Chulak mountains, and the southwestern spurs of the Altyn-Emel' range; Shnitnikov, 1936, Antipin, 1941; E. Strautman, 1953).

Farther west the range of ibex covers all of the remaining parts of the Tien Shan system, i.e., Trans-Ili Alatau, Kungei Alatau, Kirgiz (Aleksandrov), Talas, Ugam, Pskem, Chatkal', and Ferghana ranges. Evidently ibex occur even along the Kuraminsk range, at least along its eastern part, but direct proof of this is not available. Along Kirgiz range in the west ibex reach its western extremity and also along the Talas (Aksu-Dzhebogly preserve). The western limit of habitation along the Pskem and Ugam ranges has not been shown but ibex reached the western end of the Chatkal' mountains (Shavassai River, Tekeli range). Throughout the entire montane area discussed above ibex occur at suitable places eastward to the Chinese border. [174]

According to some data the range also included the Karatau (details not known) and Chu-Ili mountains, in particular Baigar promentory, Chagarla, and Dzhambyl[175] (Antipin, 1941; see below).

In the Pamir-Alai system the range covers the Alai and Trans-Alai ranges, Turkestan and Zeravshan, and also the Gissar and all of the Pamir—both its eastern and western parts.

---

[174] The range in the Tien Shan is taken from Shnitnikov, 1936; N.A. Severtsov, 1873; Spangenberg, 1936; Mashkovtsev, 1940; Kuznetsov, 1948 and 1948a; S.A. Severtsov, 1929; Kashkarov, 1927 and 1934; Tsalkin, 1950; Zarudnyi, 1915; and other sources.

[175] The place with the name Dzhambyi (Dzhambul) under discussion (974 m above sea level) lies almost straight west of the southernmost extremity of Balkhash (V.H.).

Sufficiently accurate range boundaries in this mountain system are not known, however. In the Alai mountains ibex are known in the Gul'chi region (Kashkarov, 1934), among the high mountains south of Ferghana above Shakhimardan, in the region of Kara-Kazyk Pass, and farther to the west and east (V.G. Heptner). In the Turkestan range the western limit of distribution has not been established but ibex were absent in the small mountains serving as a
547 continuation of the range into the desert, particularly in Nuratau (Meklenburtsev, 1937). In the Zeravshan range the distribution reaches at least to Pedzhakent (V.G. Heptner). The Gissar range is wholly occupied by this species, which also occupies the Baisun mountains in the south to the region of the course of the Sangardak (V.G. Heptner) and even to Zhelezny Voroty [Iron Gates] (Tsalkin, 1950; a pass from Shirabad in the Guzar between the Baisun mountains and Kugitangtau), i.e., throughout the range. The Siberian ibex is absent in Kugitangtau, despite some rather dubious data (Gureev, 1937[176]) to the contrary, and only markhor live there.

The southern boundary of the range in this region (Tadzhikistan east of the Surkhandarya), toward the Pyandzha and Amu-Darya is extremely vague. Ibex are not known from the Darvaz range (Flerov, 1935); they no doubt live on the Peter the Great range and, as pointed out already, also in the Gissar, but there are no data about the comparatively more southerly regions. It may be considered that in the highlands between the tributaries of the Amu-Darya and the lower Pyandzha, at least close to these rivers, the Siberian ibex is absent. Higher along the Pyandzha the range reaches the river.

Within the Middle Asiatic region outlined above, as also in regions described earlier, the distribution of ibex is uneven and, depending on the nature of the terrain, the distribution in separate pockets is more or less significant and isolated.

The Middle Asiatic range described above represents the reconstructed range and at some places, as mentioned already, the animal has disappeared. This is true, for example, of Ortau localities in the Kazakh *melkosopochniks* where ibex became extinct probably even in the middle of the last century. Evidently ibex are already absent in the region south of Semipalatinsk and it is doubtful that they survive in the Kalbinsk Altai' etc.

---

[176] The author at one place (p. 370) states that these ibex, according to hunters, occur "in the Karlyuk and Kuitan mountains" (Kugitangtau; V.H.), while at another place for the same region, recalling the words of the hunters, these remarks are not included (p. 361). From the author's text it is difficult to decide which of the mountain sections he had in view, especially under the name "Karlyuk".

At the same time it is possible that in the far remote past, for which no zoological data are available, ibex could have been distributed even in the Middle Asiatic region somewhat more extensively than described above. Perhaps they were more widely distributed in southern Tadzhikistan, in the western spurs and foothills of Turkestan, and the Zeravshan ranges. It is highly possible that they were more widely distributed even in Kazakh *melkosopochniks*. In general the distribution could have been slightly more extensive in the region of lower mountains and foothills (see footnote, p. 788). To a far greater extent than argali sheep, ibex exhibit philopatry and hence could have been easily destroyed in the lower mountains. This is evidently what happened even in the very early period.

The information given above on the occurrence of ibex at present in the Chu-Ili mountains and in Karatau (Antipin, 1941) has been disputed (Strautman, 1953; Tsalkin, 1950) and evidently with justification. However, there is reason to assume that the animals did live there in the past. This is more probable for the Karatau.

In 1949 six ibex were released on the northern slopes of the Palat mountains (Chatyr-Dag) in the Crimea. Their numbers rose initially but later all perished.[177]

Geographic Range outside the Soviet Union

In Mongolia the Siberian ibex is distributed in the western half of the country. Its range is not continuous and covers the mountains west of Kosogol [Hobsogol] (it is absent in eastern Prikosogol), the slopes of the Tannu-Ol, Khan-Khukhei mountains (north and east of Lake Khirgis-Nur), southern parts of the Khangai (region of the sources of the Idera, Orkhon, and Dzabkhyn) in the stretch roughly from Uliassutai (slightly northeast) to Yarbai-Here, the Mongolian and Gobi Altai in the southeast, including the Khurkhu mountains which are a continuation of the Gobi Altai. The animals are present in individual mountain massifs between the Mongolian Altai and Lakes Ubsu-Nur and Khirgis-Nur, between Khangai and the Mon-
548 golian and Gobi Altai, and along the stretch lying south of the Mongolian and Gobi Altai, and between these mountains and the state border of Mongolia with China (Adzhi-Bogdo, Tsagan-Bogdo, and other mountain ranges; Bannikov, 1954). The Khurkhu range represent the easternmost point of distribution of the species (its southeastern extremity lies roughly at 106° E long.).

---

[177] The report that their numbers reached 200 and that they were widely dispersed (Dal', 1958) is erroneous.

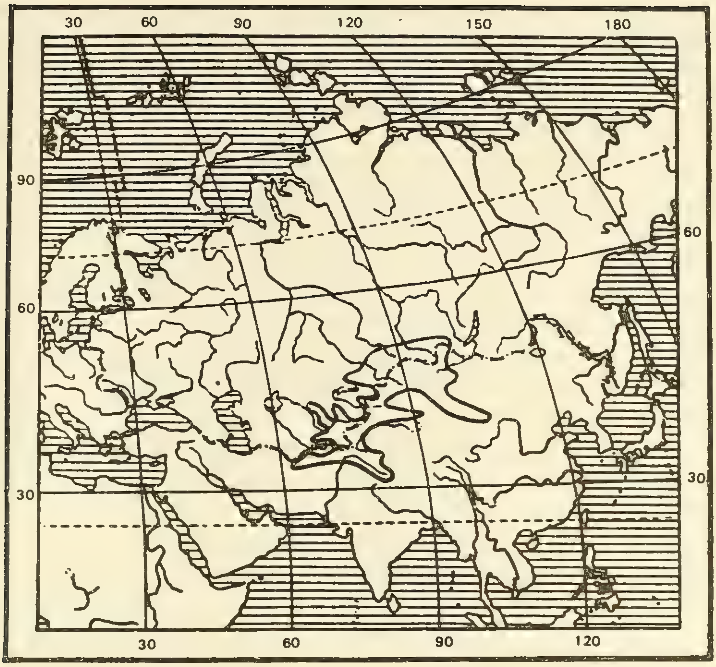


Fig. 182. Reconstructed species range of Siberian ibex, *Capra sibirica* Pall.
V.G. Heptner.

In China the range covers the extreme western parts of the country. In Dzhungaria ibex are found among the Altai, Saur, Tarbagatai, Dzhungarsk Alatau, and those uplands associated with them (details not known). Its range there represents an extension of its distribution in the USSR. The range includes the entire Chinese (eastern) part of the Tien Shan system up to its eastern extremity, Barkul', and perhaps a little farther east. The animals were also present in the mountains slightly south of Bagrash Kul.

Farther south, in Kashgariya, ibex inhabit all of the mountain ranges in the west which are continuous with Russian mountains such as Kokshaal, Sarykol'sk, and the mountains southwest and south of Yarkand, especially the Raskemdarya basin, i.e., northwestern Karakoram proper. In Keriya range, i.e., in the western part of the Kunlun system lying to the east of the Khotan meridian, the Siberian ibex evidently does not occur. Here, its geographic range does not extend east of 80° E long. Farther on its range covers all of the Karakoram and Baltistan (region of the northern bend of the Indus) and runs east along the Himalayas to Kumaon, more precisely to the vicinity of their intersection with the Sutlej and the upper reaches of the Ganges. In the Himalayas ibex are present even along the northern slope. In Tibet they are apparently absent.[178] Siberian ibex is also absent in the Pir-Panjal range enclosing the Kashmir valley on the south.

549 West of the junction of Pamir and Karakoram mountains, the geographic range of the Siberian ibex extends in the form of a long promentory into Afghanistan. Here, it covers the Hindu Kush and evidently also the Paropamisus. Westward, ibex penetrate to Herat and the Afghan Badkhiz, in particular being noted at Balamurgab on the Murgab near the border of the Soviet Union (Thomas, 1889; see above), i.e., evidently they also occupy Bend-i-Turkestan.[179] No further details whatsoever are available about the distribution of the species in Afghanistan.[180]

In northeast Afghanistan the range of Siberian ibex comes exceptionally close to that of bezoar goats inhabiting northeastern and eastern Iran and Gyaz'-Gyadyk in the east of southern Turkmenia. It is possible that they even contact each other there. However, there may not be any significant overlapping of the two ranges.

In a much larger part of Afghanistan, Siberian ibex live in the same territory as markhor (*C. falconeri*). In practice, evidently, much of the distribution of markhor (apart from the south) coincides with that of Siberian ibex. No information whatsoever is available about the nature of the ecological relations of these two species in this country, how closely individuals of the two species live, or how large is this common territory. In the higher parts of the Hindu Kush system, probably only Siberian ibex occur while, at the lower levels with which markhor are more associated, coexistence of the two species under favorable conditions is quite possible (see information given above for Afghan Badkhiz; details may be seen in Heptner, 1956). In any case the overlapping of territory over much of the area is indisputable.

---

[178] Information about distribution in the Himalayas is contradictory but the actual position is evidently as described above. This is particularly confirmed by the latest data (Prater, 1947). Information about the occurrence of ibex in the east farther than the place referred to, i.e., right up to the region north of Sikkim and even Shigatse in Tibet, is evidently erroneous.

[179] In spite of the fact that the range of the Siberian ibex comes very close here to the Soviet boundary, no positive information is available of the penetration of this species into southern Turkmenia. Nevertheless ibex could quite possibly be seen even as stragglers in the Soviet highland regions between Kushka and Murgab (Chengurek mountains) and possibly even in the Karabil' highlands east of Murgab.

[180] The description of the range outside the USSR is the result of modification—corrections and additions—of the data available in literature cited by Tsalkin (1950).

The information given above excludes the possibility of considering these two forms only races of the same species; such suggestions (Schwarz, 1935; see characteristics of the genus *Capra*) are clearly based on inadequate knowledge not only of morphological but also of factual geographic data.

It is possible that in the past some small overlap in the ranges occurred in Tadzhikistan also (Darwaza range), where both species are found today. (V.H.)

Geographic Variation

More names have been given to the Siberian ibex than to any other species of the genus, which has greatly complicated the study of its geographic variation. The reason for this is the extreme individual variability of color and size, mainly the horn structure, to which maximum attention was paid. Erroneous theoretical views of some researchers have also played a notable role.[181] There are almost 20 formal names for this species today.

Until recently 13 subspecies of Siberian ibex were acknowledged; of these, 6 occur in the Soviet Union (Lydekker, 1915), but this
550 number is clearly an exaggeration. The characterization of these forms is very weak, and for the most part unsatisfactory; their type localities partly coincide or almost coincide, and so on. In 1935 all the forms of the species described until then were reduced to two, i.e., *C. s. sibirica* of the Altai-Sayan, also inhabiting the Mongolian mountains, and the Tien Shan-Himalayan *C. s. sakeen* covering the remaining geographic range (Flerov, 1935). These are distinctly differing groups in external and craniological characteristics. Somewhat later this revision was criticized as an extreme simplification of the prevailing situation and a minimum of six forms recognized in the species. Of these, two were described as new (Tsalkin, 1950).

---

[181] For example, Noak (1902), following Vach and Hagenback, considered that each mountain range separated from others by deserts, or more generally, plains, or even broad valleys should have its own form of goat. Even deep gorges were recognized as adequate isolators. Thus Noak (1902) thought that in the Caucasus the two species of tur (Dagestan *C. cylindricornis* and Kuban *C. caucasica*) were separated and isolated by Daryalsk gorge, as if it were impenetrable for these animals! Western researchers not well versed in the geography of Russia and Central Asia, introduced absurdities such as the description of five forms from the Altai and the Sayans, especially one from Pri-Irtysh Altai and another from Lake Telets (see synonyms). Along with the natural errors committed in the early stages of the study of the geographic variation of animals, the fantastic systematic and zoogeographic concepts of the Berlin zoologist Matschie, considered an authority in his time, played no mean role in this confusion.

Three subspecies were acknowledged for the Soviet Union—Altai-Sayan *C. s. sibirica,* Tien Shan-Pamir *C. s. alaiana,* and *C. s. formosovi* distributed in the Kirgiz ranges. Most recently in the entire group of Siberian goats only one form has been acknowledged, i.e., *sibirica* (as a subspecies of *C. ibex;* Ellerman and Morrison-Scott, 1951; Haltenorth and Trenze, 1956). This viewpoint is unacceptable. The scheme of Flerov (1935) is better justified, at least insofar as Soviet forms are concerned. For the species as a whole this scheme could, however, be somewhat simplified.

The following forms may be recognized in the USSR:

1. Altai Siberian ibex, *C. s. sibirica* Pallas, 1776 (syn. *pallasii, lydekkeri, altaica, fasciata, typica, lorenzi*).

Size relatively small. Maximum (total) skull length of adult males 256 to 293 mm (M 270) and of females 239 to 260 mm (M 247). Nasals short; their absolute length in males usually not more than 100 mm, constituting 28 to 37% and 32 to 42% of total skull length in males and females respectively. Anteronasal suture (viewing skull from above) falls in front of anterior rim of orbit, or even with it.

Horns of males relatively short and not thick. Length along curvature usually does not exceed 100 cm; basal circumference 18.5 to 24 cm (M 20.7).

Winter coat of adult males light-colored (already described above).

This form occurs in the Altai and the Sayans. Outside the USSR it is found in Mongolia except, evidently, in the Gobi Altai and mountains of the Trans-Altai Gobi.

2. Middle Asiatic Siberian ibex, *C. s. alaiana* Noak, 1902 (syn. *almasyi, transalaiana, merzbacheri, formosovi*).

Larger than nominal form. Maximum skull length of adult males 276 to 306 mm (M 292) and of adult females 248 to 262 mm (M 254). Nasals long; their absolute length usually exceeds 100 mm and comprises 32 to 40% and 34 to 43% of total skull length in males and females respectively. Anteronasal suture (viewing skull from above) falls behind anterior rim of orbit.

Horns relatively large and massive. Length along curvature exceeds 100 cm; basal circumference 20 to 28 cm (M 23).

Winter coat of adult males dark cinnamon-brown. Light-colored spot in the form of a saddle occurs on the back; form and size of spot vary or spot sometimes absent.

This form occurs in the Tien Shan and Pamir-Alai systems. Outside the USSR its distribution is not known; evidently it is also found in the eastern (Chinese) portion of Tien Shan.

Some systematic and nomenclatural details of this form are not clearly understood. In relation to the nominal form its morphology has been characterized extremely well. At the same time all its features essentially coincide with those characteristic of the Himalayan form *sakeen*. Geographically the Soviet populations, for example the Pamir live in the immediate proximity of the range of the form *sakeen* and are separated not by hundreds but only several tens of kilometers. Thus, the Russian Pamir-Alai and Tien Shan ibex should probably be merged with the Himalayan form *sakeen,* as done by Flerov (1935).

This is not done here only because to date no one has compared the Soviet Middle Asiatic ibex with the Himalayan. At the same
551 time, it is theoretically possible that they could differ in some respects. This may be applicable, however, to Tien Shan forms, and extremely dubious with respect to the Pamir-Alai ibex. Yet it has been shown (Tsalkin, 1950) that both Russian forms are essentially identical. For these reasons the separation of the Russian Middle Asiatic form from *sakeen* is purely tentative here.

Tentatively, the name *alaiana* (see footnote, p. 774) is being retained for ibex from the Pamir-Alai system. The next valid name is *almasyi* Lorenz with terra typica in the Tersk Alatau in the Tien Shan system, i.e., in mountains farther separated from the terra typica of the form *sakeen* than from the form *alaiana.*

The form *C. s. formosovi* with its range in "Kirgizia range, Talassk Alatau, and other ranges of the western Tien Shan" (Tsalkin, 1950) has been shown to differ in only one distinctive feature from the forms distributed in other parts of Tien Shan, i.e., in the absence of a light-colored saddle spot in the winter coat of males. But this characteristic is not a reliable feature: in the western Tien Shan there are specimens with a saddle spot and, contrarily, in the eastern and southern parts of the Middle Asian mountains animals without it. In any case this form requires substantial data for its justification.

The taxonomy of ibex outside the USSR has been studied even less well since nothing is known about the characteristics of Afghan animals. Evidently, however, there are two forms: *C. s. hagenbecki* Noak, 1903 from the Gobi Altai and the highlands of the Trans-Altai Gobi, which is very close to *C. s. sibirica* of the Altai, and *C. s. sakeen* Blyth, 1842 to which the Soviet Middle Asiatic ibex are quite close. The Afghan ibex inhabits all of the southern and southeastern parts of the range of the species outside the USSR. The rest of the names assigned to these animals from Kashmir, Gilgit, Baltistan, and Lahaul, i.e., from places which are close to each other, are evidently synonyms of the form *sakeen* or of the Soviet Middle

Asiatic form. The same is true of the form *dementievi* Zalkin, 1949, described from the region southwest of Yarkand. (V.H.)

Biology

Population. The population of Siberian ibex is still fairly high in the Pamir and in adjoining parts of the Tien Shan. In the mountains of the western and central Tien Shan they are particularly abundant in the Talas Alatau, the Kirgiz ranges, and Tersk Alatau. They are preserved in significant numbers in the northern Tien Shan (Kungei-Alatau and Trans-Ili Alatau) and at places in the Dzhungarsk Alatau. In the Tarbagatai, Altai, and Sayans, ibex are fewer (Tsalkin, 1950; Afanas'ev et al., 1953). In the mountains of the western and central Tien Shan, and also in the Dzhungarsk Alatau, herds of 120 to 200 ibex are often encountered in autumn (A.A. Sludskii).

Yet several authors have pointed out that even in those regions of the Soviet Union where ibex are relatively abundant even now, their populations were two to three times greater at some places as late as the early 1940's. Ibex stocks have been adversely affected by intense and irrational hunting; adverse consequences have also accrued from grazing a large number of domestic goats, sheep, horses, and yaks in pastures used by ibex. The ibex population has also been depleted in some areas (Kirgizia) by epizootic scabies (Dubinin et al., 1958; A.A. Sludskii).

Accurate data on ibex populations are available for a few regions. In the Bol'shoi Kyzylsu river basin (Tersk Alatau) 550 Siberian ibex inhabited an area of 200 km^2, of which 170 km^2 were suitable for them, in the summer of 1949, corresponding to 27 to 32 animals per 1,000 hectares. In the summer of 1950 in three valleys of the eastern Pamir (Dzhaanbai, Mukor-Chichekty, and Bilyand-Kiik), there were 600 ibex in an area of about 100 km^2; in some valleys their population density varied from 40 to 90 or 110 animals per 1,000 hectares of area suitable for ibex habitat. Lower along the course of the Bilyand-Kiik, where a precise census was not carried out, ibex were even more numerous (Egorov, 1955). Egorov has also pointed out that in the regions visited by him in the western Pamir
552 (Khorog, upper course of the Vancha, and others), the ibex population was not large, far less than in the eastern Pamir.[182] This could possibly be explained by the smaller number of suitable sites available there for habitation by ibex.

---

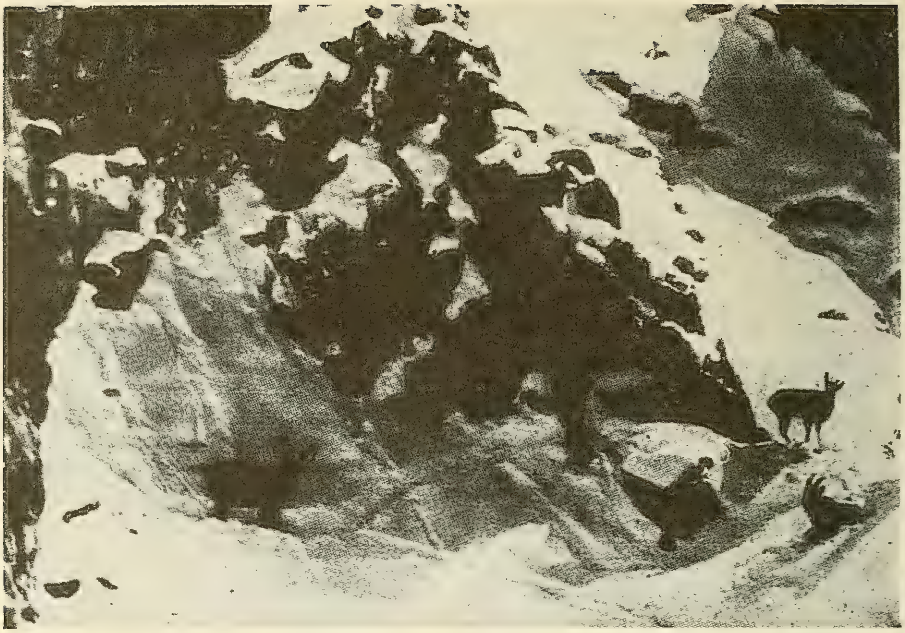
[182] According to Meklenburtsev (1949) Siberian ibex were more numerous in the western than in the eastern Pamir.

In the early 1930's an ibex population density of 62 animals per 1,000 hectares projected on mountain slopes was considered typical of the Bashkaus basin (eastern Altai) in winter; it would have been significantly less in summer when ibex dispersed widely (Dmitriev, 1938).

For the Soviet Union as a whole the population of Siberian ibex is more than the population of all the remaining members of genus *Capra* taken together and totals more than 100,000 animals.

Habitat. Ibex inhabit a broad belt of the mountains from 500 to 4,500 or 5,000 m above sea level, often ascending even higher (Pamir). However, in a given region they are usually confined to a narrower belt. Unlike most wild sheep, which prefer more gentle relief, Siberian ibex, like other species of this genus, are attracted to montane areas with precipitous slopes abounding in cliffs and rocky talus. In the forest zone of the mountains, ibex are encountered only at places where the relief is steep and rocky and the slopes bereft, or almost so, of trees. Ibex seek refuge among rocks from wolves, especially at places where they are highly persecuted; ibex beds among rocks are not uncommon. Ibex graze in meadows covered by low alpine (above timberline) or steppe vegetation and have often been sighted on comparatively gentle slopes, sometimes 500 m or even farther away from the nearest rock. Shallow snow is characteristic of most ibex habitats, especially in winter. Ibex avoid areas with soft soil (Dmitriev, 1938; Tsalkin, 1950; Egorov, 1955).

In the Pamir, where the permanent snow line is at a high level and human settlements occur high in the mountains, ibex are distributed mainly in 3,000 to 5,000 m zone of the mountains. In the 553 Gissar and Trans-Alai ranges ibex live most of the year in the alpine zone (Leviev, 1939; Kuznetsov, 1937). In different parts of the western Tien Shan ibex live in the montane zone of 1,000 or 2,000 to 3,500 or 4,000 m (Shul'pin, 1948; Abduldabekov, 1949); for example, in Aksu-Dzhabaglin preserve they are found in summer in the upper parts of the forest belt and are numerous in the subalpine and alpine zones. In the southern part of the central Tien Shan (Tersk Alatau and Khan Tengri) ibex are confined to heights of 2,700 to 3,500 or 4,200 m (Antipin, 1946; Zimina, 1953; and others). In the Kungei-Aksu-Dzhabaglin preserve they are found in summer in the upper tau (northern Tien Shan) the majority of the ibex population lives in the snowfree period of the year above timberline (2,500 to 4,000 m), but animals are encountered the year round in the Syugata River valley at about 1,500 m (Shnarevich, 1948; and others), while in the Bol'shoi and Malyi Bogutas, and in the Altyn-Emele they are even lower—at an elevation of 600 to 800 m (A.A. Sludskii). In the Altai



552 Fig. 183. Siberian ibex on the Tersk Alatau range in their winter habitat. Winter of 1948/49. Photograph by N.N. Nemnonov.

and Sayans ibex inhabit the forest belt characterized by steep slopes of deep gorges (not below 500 m above sea level) and also live high in the mountains (3,000 to 3,500 m). The vertical distribution of ibex in Mongolia ranges from 700 to 4,000 m (Bannikov, 1954). Thus the opinion that the habitats of Siberian ibex are confined mainly to higher altitudes is true only of some montane regions. This species is primarily an inhabitant of cliffs.

Over a significant extent of the range of Siberian ibex their winter range is lower than their summer range. Adult males usually reside higher among mountain slopes than females with young.

Food. The food of ibex has not been adequately studied. On the whole for Middle Asia and southern Siberia it has been established that goats consume up to 80 plant species. In summer they eat mainly green herbaceous vegetation, most avidly grasses (meadow grass, sheep's fescue, wild barley, foxtail, *Reogneria,* and others), some sedges (*Kobresia* and several species of genus (*Carex*), cinquefoil, *Oxytropis,* Bokhara vine, anemone, sagebrush, tansy, buttercup, and other species of forbs; onion is also well consumed. In the stomach of an ibex killed at the end of July in Noyan-Bogdo (Mongolia) onion constituted 60 to 63% of the volume of stomach contents (Bannikov, 1954).

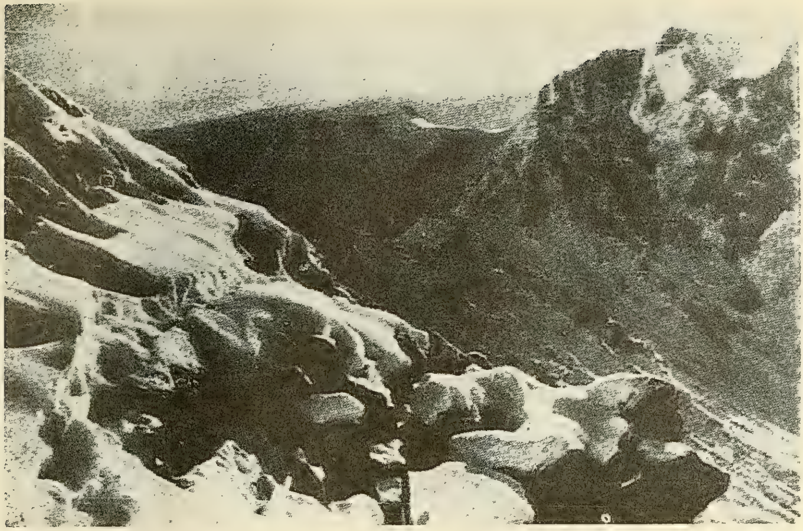


Fig. 184. Winter habitat of Siberian ibex in Tersk Alatau range. An ibex trail is visible at the left. Winter of 1948/49. Photograph by N.N. Nemnonov.

554 In the Trans-Ili Alatau ibex consume in summer, apart from herbaceous vegetation, shoots of juniper and *Ephedra* (Shnarevich, 1948), and in the Dzhungarsk Alatau young leafy twigs of spirea and tulip leaves (A.A. Sludskii).

The autumn food of ibex is similar to the winter food in composition; along with herbaceous vegetation it includes thin twigs of some shrubs and trees, their fruits, especially those of dog rose, some species of currants (in the Altai sour berries of *Ribes hispidulum* are well consumed from the second half of summer; Dmitriev, 1938), and mountain ash. The bulk of the stomach contents of three ibex caught in autumn in the Pamir consisted of the seeds and stalks of prangos and Bokhara vine (Egorov, 1955).

Depending on the depth of the snow cover and nature of the vegetation, ibex feed in winter mainly on herbaceous stalks (grasses, sedges, sagebrush, and some others) and partly on the green portions of plants, or a considerable quantity of twigs, bark, buds, needles (of juniper), and dry leaves of trees and shrubs: honeysuckle, willow, meadowsweet, wild cherries, caragana [pea shrub] mountain ash, dog rose, *Ephedra,* and other plants (Dmitriev, 1938; Shnarevich, 1948; Shul'pin, 1948; Egorov, 1955). The stomachs of eight ibex caught from October through April in Alma-Ata preserve, contained roughly of 75% (by weight) shoots, leaves, and needles of various

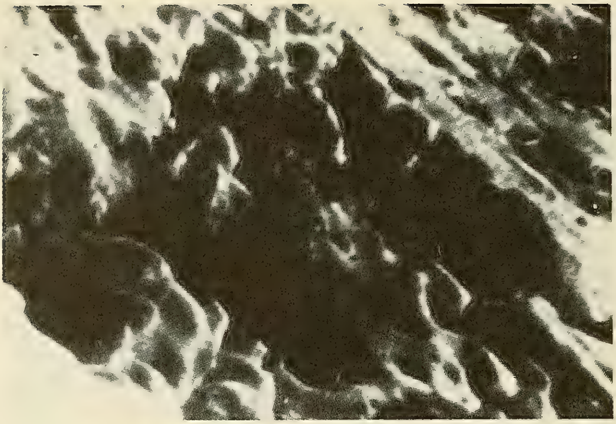


Fig. 185. Snow dug through by Siberian ibex while feeding on standing dead vegetation in a winter pasture. Tersk Alatau. Winter of 1948/49. Photograph by N.N. Nemnonov.

shrubs, mainly *Ephedra* and juniper,[183] which were found in every stomach (Shnarevich, 1948). In the eastern Pamir, as long as the snow is not deep, goats feed mainly on sedges; later, when this becomes difficult of access, they shift to feeding on sagebrush and *Eurotia ceratoides* (Meklenburtsev, 1949).

The importance of standing dead vegetation and shrubs in the winter diet varies, and depends on the snowiness of any given winter (Egorov, 1955). Standing dead vegetation is consumed in snowfree areas or dug up with the hooves from under the snow at places where it is not excessively dense and no more than 30 to 40 cm deep (R.P. Zimina). In some regions ibex in winter often consume arboreal and possibly terrestrial lichens.

According to the calculations of Egorov (1955) in one day females consume 8 to 10 kg of green fodder and large males up to 16 kg; these values correspond to double the maximum weight of their stomach contents.

Goats visit dry argillaceous salt licks where they swallow particles of fine earth, sometimes creating small holes on the slopes (Dmitriev, 1938; Nasimovich, 1949). In the eastern Pamir, along with grass they swallow salt, encrustations of which are common on the slopes (Egorov, 1955). Salt licks are visited the year round. If the food is sufficiently succulent or other moisture sources available

---

[183] In the Tersk Alatau and western Pamir mountains juniper is not eaten (Egorov, 1955).

(dew, snow, etc.), the animals can remain without water for many days.

555 *Home range.* The size of the home range can only be tentatively conjectured. In summer, depending on herd size and availability of pastures, shelters, etc., daily movements occur over 500 to 5,000 hectares, rarely over larger areas; the extent of daily movements varies from 3 or 5 to 15 or 20 km. Ranges of individual herds are evidently not isolated for much of the year and instead widely overlap. At the same time the home range and paths of daily movements of individual herds over a longer period (a few weeks) remain fixed. In some areas of the mountains up to 60 to 100 or even more animals live per 1,000 hectares of area when living conditions are suitable (see section "Population"). The extent of daily movements, like the size of the home range, is usually less in winter than in summer.

Daily activity and behavior. The following daily activity is characteristic of Siberian ibex in summer. They move out from beds before sunrise to pastures, where they remain until it warms up (10:00 to 11:00 a.m., and roughly midday on the higher levels of the Tersk Alatau and in the eastern Pamir). After this they retreat to beds to escape weather conditions, possible danger, and so on. Beds are made under overhanging cliffs, in snow, or sometimes on open slopes on rubble or grass. From 4:00 to 5:00 p.m. grazing resumes, which continues with intervals into the night. Judging from observations made in the Tersk Alatau and eastern Pamir, ibex take a prolonged rest on summer nights only from midnight onward, rising an hour before dawn (Egorov, 1955). Thus the daily cycle of activity of ibex consists of a fairly regular alternation of grazing and rest, which is quite characteristic of these animals throughout their range in the Soviet Union.

Depending on the nature of the relief, distribution of pastures, presence of cattle in them, daily fluctuations of temperature, and other conditions, the sites of nocturnal and diurnal residences of ibex may be close to each other or at a distance of 5.0 to 8.0 km apart. Quite often the sites of nocturnal residences are at a significantly higher level than the diurnal, sometimes by 500 m (reckoning vertically) or even more; there is, however, no fixed pattern. Sometimes both are at the same height or the nocturnal site lower down the slope. While grazing, the animals keep on the move, often in one direction, going away from rocks for 500 m or more. When gadflies and blood-sucking insects are numerous, ibex lie on the snow to rest and move onto windy slopes. Ibex visit water holes irregularly, at intervals of several days; they visit salt licks also, but not daily.

The daily cycle of activity of ibex described above can be seen more distinctly on warm summer days. In the event of rain and mist, periods of grazing and rest are not limited to any definite hours of the day. During the day the animals graze longer and rest less, lying down only after their stomach is full for ruminating (Egorov, 1955). In spring, autumn, and especially in winter the period of daytime grazing is more protracted and the rest period shortened. In the snowy period of the year, when gathering food from under the snow requires considerable time, ibex graze throughout most of the daylight hours (Dmitriev, 1938; Egorov, 1955).

The body and legs of ibex are excellently adapted to movement on rocky and very rugged terrain, where they can run fast over a short distance. Utilizing insignificant rock projections goats can negotiate almost perpendicular slopes, facilitated by the elastic and fibrous pad of their hooves and the rim of horny matter around them. Such a hoof structure also minimizes slippage on dense firm snow and even on ice (Golovnin, 1901; and others).

The weight load on the hoof is considerable, 550 to 950 g per sq cm, with an average of 850 g per sq cm of contact surface in ibex 556 from central Tien Shan. They easily negotiate soft snow no more than 20 cm deep but that up to 30 to 40 cm with difficulty. When the snow cover is thicker, movement becomes extremely difficult and the animals do not leave their trails unless compelled to do so (Zimina, 1953).

During snowstorms ibex shelter under rocks or descend far into gorges; on open slopes they wait for the inclement weather to clear, remain in their beds, and are covered by snow up to their horns (Shul'pin, 1948; and others).

Ibex are good swimmers. At the end of November, 1928, six ibex reportedly swam across the upper course of the Yenisey (below the mouth of the Kara-Kem River) at a time when dense slush ice was present in the river (Belousov, 1929).

Hearing, smell, and vision are well developed in ibex.

Ibex live in groups of 3 to 40 animals, which often merge into large herds of up to 100 or 200 or even more, which readily split into smaller groups. Large herds are more common in regions where ibex are abundant. Such herds, especially if they are comparatively large (30 to 40 animals), usually comprise animals of both sexes and of different ages. Some adult males (4 to 5 years old), except in the period of rut and for a month thereafter, live in isolation but more often in groups of not more than 10 animals, selecting for this purpose the least accessible mountain regions (Egorov, 1955; and others).

Gregariousness is highest at the end of winter and in spring, and later in autumn, in September and October. Before parturition females break away from mixed herds into small groups. Seven to ten days after parturition females which have separated from the herd, rejoin it. Mixed herds break up for the second time early in winter when "harems" are formed (Egorov, 1955; and others).

Seasonal migrations and transgressions. In many parts of their range ibex are characterized by seasonal migrations, best manifested in high mountain regions with an unfavorable snow cover regime or under conditions of generally severe winter. In winter ibex descend the slopes and often move over to other ranges. The animals select steep, low-snow slopes, mostly with southern exposures or those close by as wintering sites. Occasionally they settle in shaded sections where the snow is deeper (but blown away by wind from part of the slope), but where the quality of available food is better. The range of vertical migrations varies from 200 to 300 m (Pamir and some central Tien Shan ranges) to 1,500 to 2,000 m (Gissar range, Talassk and Trans-Ili Alatau, and the high-montane Altai), while the overall distance covered ranges from 1 or 3 to 20 or 30 km. Depending on winter conditions, all the ibex winter in the alpine zone (Pamir, Tersk Alatau, Khan-Tengri) or only a few while the remainder descend to the forest border. In particularly snowy winters they move even lower down, into the montane forest zone (Gissar range, central parts of Talassk Alatau, Dzhungarsk Alatau, high-montane Altai, and eastern Sayan). In the western part of the Talassk Alatau (Aksu-Dzhabaglin preserve), in the mountains of Trans-Ili Alatau and in the western Sayan, almost all ibex, even in normal winters, descend into the forest zone (Nasimovich, 1955). In the Altai, Sayans, and at some places in the Tien Shan mountains,
557 some live year-round in the montane forest zone at low elevations. Seasonal migrations of ibex in these regions involve minor shifts (up to 1 to 3 km) from one place to another.

Return to wintering sites in the Tien Shan mountains occurs mostly in November (in the event of a late winter, only in December and even in January), and in the Altai in October. The main stimuli to trigger migrations are usually heavy snowfall or a sharp temperature drop (Nasimovich, 1955). Females with kids are the first to move down the mountainside.

In some regions of the central and western Tien Shan excessive snowfalls are common in the upper mountain levels in February or March of almost every year and force many ibex to migrate even lower down the slopes.

In the eastern Pamir in autumn, after cattle are driven away from upland pastures, most ibex (animals with winter coat still not

556 Fig. 186. Winter range of Siberian ibex in the Tersk-Alatau range. Winter of 1948/49. Photograph by N.N. Nemnonov.

grown) descend at night lower on the slope to the winter range. Nocturnal frosts are not as intense lower down as higher up in the hills, where the temperature may fall to −15 to −18°C. Between 10:00 and 11:00 a.m., ibex reascend the hills (Egorov, 1955).

In spring movement up into the mountains begins as the thawed areas enlarge, commencing around mid-April, and at some places even in March. The first to climb to the summer pasture level are old males, which may be seen there in May. Females with kids, which are less resistant to cold (Egorov, 1955), as well as males up to four to five years of age reach there later, most often in July. In summer, in the event of prolonged unfavorable weather accompanied by snowfalls, many ibex move down temporarily.

Apart from climatic and other factors, pasturing of domestic cattle, intense persecution by hunters, and to a lesser extent bloodsucking insects and gadflies exert considerable influence on the nature of seasonal migrations. Instances are known of summer migrations of ibex to distances up to 20 km (Shnarevich, 1948).

Reproduction. Information about the periods of rut in ibex is contradictory. There is no doubt that this is explained not only by inadequate study of the subject but also by the fact that in different parts of their range and also at different elevations, rut sets in at different times; moreover its onset and duration depend greatly on weather characteristics. Judging from the data of various researchers, goats become sexually aroused in November in the eastern Altai, at the end of November to December in the Kungei-Alatau, Trans-Ili Alatau, and eastern Tien Shan, and in December to early January in the Sayans,[184] southern Altai, central Tien Shan, and Pamir. In Aksu-Dzhabaglin preserve (Talassk Alatau) rut is more often observed from November 25 to December 5, slightly earlier in a good autumn and later in a bad one. In general, the commencement of rut in this region varies within ten days. Copulation occurs for about one week (Shul'pin, 1948). A relatively short duration of rut (not more than 10 to 15 days) has been reported for the Tersk Alatau and eastern Pamir (Egorov, 1955). In the eastern Altai the duration of the period of rut is reckoned as three weeks (Dmitriev, 1938) and in the Trans-Ili Alatau one month[185] (Shnarevich, 1948).

Powerful adult males aged not less than 5 to 6 years take part in reproduction and form harems of 5 to 15 females, which they guard from other males. During rut combats are common among males but deaths are extremely rare.[186] During rut males eat little and their condition greatly worsens.

At least some ibex become sexually mature at 1.5 years of age; some females bear kids at the age of 2 years; males of that age do not mate since they cannot successfully challenge the more powerful adult males (Tsalkin, 1950; Egorov, 1955). In the eastern Pamir and
558 Tersk Alatau a significant percentage of females give birth only at the age of three years (Egorov, 1955). In a yearling male caught in November in the Tersk Alatau no sperm were found in the testes (Rumyantsev, 1935).

Gestation lasts 170 to 180 days. In different parts of the range, depending on the period of estrus, kidding takes place from the end of April to around June 20, but mostly in May. In 1958 in the eastern spurs of the Dzhungarsk Alatau (Ton-Dzhailyau mountains) the first post-partum female was caught on May 11; the last of nine pregnant females taken in May of the same year was killed on May 26 (E.F. Savinov and A.A. Sludskii). From 1935 to 1945 in the spurs of the Trans-Ili Alatau (900 m above sea level), kidding occurred from May 1 to 25 (A.A Sludskii). In the Tersk Alatau and Pamir, in conformity with the much later periods of rut there, females give birth in June. For example, in 1950 in the eastern Pamir mass kidding occurred from June 10 through 20; the last birth was on June 24 to 25 (Egorov, 1955).

---

[184] According to Belousov (1928) rut in ibex in the western Sayan is not in December, but November.

[185] This reference contradicts the data of the same author (Shnarevich, 1948) that the period of kidding of ibex in the Trans-Ili Alatau continues for 1.5 to 2.0 months.

[186] such an instance was described by Shnarevich (1948).

Kids usually number one or two (twins are delivered by some adult females and, as a rule, a single kid by young females); triplets are very rare. Not only triplets but even twins are quite rare in nature. Of the 56 pregnant females caught in the central Tien Shan and Pamir, only two bore twins; the rest produced a single kid each. Of nine pregnant females caught in the eastern spurs of the Dzhungarsk Alatau in 1958, only one contained two fetuses, while the rest had one each (E.F. Savinov and A.A. Sludskii). In the Leningrad Zoological Garden, where food conditions are roughly uniform throughout the year, even young females usually bear twins (Egorov, 1955). There is a case on record from Kirgizia of a pregnant female caught in 1938 with four fetuses already covered with wool (D. Dement'ev et al., 1956).

No less than 15 to 20% adult females (sometimes, evidently, far more) remain barren. This may depend on several factors. Old males gathering large harems are evidently incapable of mating with all the females (Egorov, 1955). In the event of unfavorable weather the activity of animals in the period of rut decreases. When winter is particularly severe, some pregnant females abort (Shul'pin, 1948). Barren females are often young.

Growth, development, and molt. Newborn kids in the Trans-Ili Alatau weigh 3.5 to 4.0 kg (Shnarevich, 1948).[187] On the very first day of life kids can follow after their mother but only for a short distance (Egorov, 1955). Usually kids lie concealed among stones and shrubs, revealing little mobility for the whole of the first week after birth. Suckling extends up to autumn, sometimes even longer. A lactating female was caught at the end of December (Shnarevich, 1948). The young begin to eat grass at the age of one month or slightly earlier. They move with their mothers until the arrival of the next generation, often even a little longer, but usually maintain themselves separately during the periods of rut and calving.

Growth is most intense in the first year of life. Young males and females maintained in the Alma-Ata Zoological Garden for 36 days from mid-September added from 16 to 20.1–20.4 kg to their weight, while a year-old male from early June in less than six months increased from 32.7 to 50.0 kg (Zverev, 1948). Compared to males, a perceptible lag in growth is manifested in female body size at one year of age. Body measurements continue to increase, even after the onset of sexual maturity, up to the age of eight years according to Shnarevich (1948).

---

[187] In related species, i.e., Alpine ibex *Capra ibex*, newborns weigh 1,470 to 4,200 g with an average of 2,870 g. Kids of two-year-old females usually weigh less than 2 kg; they have less vitality and often die (Meyer-Holzapfel, 1958).

Among 40 ibex caught in the Tersk Alatau and Pamir only in one case did the weight of a male, apparently not determined very accurately, exceed 80 kg; the other males weighed no more than 76.7 kg, and females, 55.6 kg (Egorov, 1955). An adult male caught in May, 1958, in the Dzhungarsk Alatau, less well nourished than normal, weigh 80.2 kg (E.F. Savinov and A.A. Sludskii). Some individual females from the central and western Tien Shan reach 60 kg while males exceed 100 kg (according to some references, up to 130 kg). Ibex from the Altai and the Sayans are smaller (Tsalkin, 1950).

559 Horns begin to grow within the first few days of birth and are distinctly seen by three to four weeks. The first (hyaline) horns are sloughed by winter, exposing the permanent horns. In males horns lengthen more intensely in their second year and continue to grow in volume from 4 to 8 or even up to 9 to 10 years. Ring formation is due to the alternation of intense growth of the horny sheath in the snowfree period of the year, when the animals feed copiously, and near total cessation of growth in winter. The main features of this type of horn development are evidently typical of all members of the genus *Capra* (Tsalkin, 1950).

In spring, depending on climatic and other conditions, ibex molt from March–mid-May to early June–mid-July. Late molting seasons are characteristic of the high-montane regions of the central and eastern Tien Shan and Pamir. In the Talassk Alatau ibex begin to molt in April. A male five years old caught on April 24, 1941, in the Kirgiz range at a height of 3,500 m was molting intensely (A.A. Sludskii). Molt commences earlier after less snowy winters, especially in the event of a warm spring, and commences late after a severely cold snowy winter. Shedding (underfur and part of guard hair) commences from the region of the scapula, shoulders, thighs, and cheeks, then extends to other parts of the body. The first to molt are males, barren females, and juveniles, while the last to molt are females which have given birth. In the latter, remnants of winter hair are sometimes preserved on the spine and nape up to the end of August. Molt is also delayed in sick animals and in those heavily infected with parasites. The last to shed is part of the winter guard and intermediate hair, under which short summer hair up to 2.0 to 3.0 cm can be seen in June (in Pamir and Tersk Alatau) (Shnarevich, 1948; Shul'pin, 1948; Egorov, 1955; and others).

In August–September (earliest in the Pamir and central Tien Shan) a dense underfur is visible under the summer hair; a few weeks later the winter guard hair begins to grow and in October and November covers the underfur and summer hair. Summer hair is not shed (references to such are erroneous) but preserved in winter in the form of reddish-colored intermediate hair (Egorov, 1955). In autumn the first to don winter pelage are adult males and females without kids (Shul'pin, 1948). Ibex are in full winter coat in December.

Judging from horn rings, female ibex in nature rarely live to 16 or 17 years, and males 15 years. In the Leningrad Zoological Garden ibex have survived for 18 to 20 years (Egorov, 1955). Females of Alpine ibex held in the Bern Zoological Garden remained fertile up to the age of 17 years (Meyer-Holzapfel, 1958).

Enemies, diseases, parasites, mortality, competitors, and population dynamics. The predators posing maximum danger to ibex are gray wolf, snow leopard, and golden eagle. Damage by wolves is particularly significant in the latter half of winter, when males older than four or five years, weakened during the period of rut and barely surviving the snowy winter, make easy prey. In one region in the western Pamir, on valley slopes covering a total of 14 km remains of 11 ibex (all males aged 6 to 11 years) attacked by wolves were found. The remains of another 30 ibex (22 males and 8 females; of the former, 64% were older than four or five years) killed by snow leopard were found in the same area. In herds there males older than six years constituted 29%[188] of all the animals of that sex, which points to selective attacks on old male ibex by predators (Egorov, 1955). The snow leopard also inflicts much damage on ibex in the mountains of the Dzhungarsk, Trans-Ili,and Talassk Alatau. From 1933 to 1935 in Aksu-Dzhabaglin preserve the summer feces of snow leopards consisted predominantly of remains of kids (Skul'pin, 1948). In regions where snow leopards are relatively more numerous the ibex population is reduced (Afanas'ev et al., 1953).

560 Judging from bones found around nests of golden eagles, these birds exclusively attack young ibex (Egorov, 1955). References to instances of three adults killed by golden eagles (Belousov, 1934; Dmitriev, 1938) appear dubious. Secondary enemies of ibex are red wolves (in most regions they are rare), lynx, wolverine (instances of its attack on ibex have been reported in the Altai and Sayans), and

---

[188] In several valleys of the eastern Pamir males older than five years constituted 2.0 to 13.2%, or an average of 9.8%, of all ibex of both sexes older than one year (Egorov, 1955).

the red fox which attacks weak kids. References to the destruction of kids by lammergeier have not been confirmed by observations and are evidently unreliable (Egorov, 1955; and others). Bears attack kids very rarely.

In zoological gardens of the Soviet Union ibex have been found to suffer from necrobacillosis, pasteurellosis, malignant catarrhal fever of cattle, and other diseases. Ibex suffer from necrobacillosis even under natural conditions. A large number died in the Pamir from an epizootic disease called "kara-yupka" (black lung) by the local people (Meklenburtsev, 1949). According to Sludskii (1954) this disease was infectious pleuropneumonia.

Over 20 species of helminths have been detected in ibex. Of these, roughly three-fourths were nematodes and the rest cestodes and trematodes. Most of the species are commonly found in domestic and other species of wild ungulates. The most pathogenic is the pulmonary nematode *Cystocaulus vsevolodovi,* which is found extensively among ibex in the Syugata region (Trans-Ili Alatau) (Vsevolodov and Boev, 1948; Boev and Sokolova, 1949; Shnarevich, 1949; Boev, 1957).

Some species of coccidians of the genus *Eimeria* have been detected in ibex (Svanbaev, 1958; and others). A Siberian ibex suffering from coccidiosis was found in the Tbilisi Zoological Garden (Sarkisov, 1944). Ibex suffer from oxbot (*Oesterus caucasicus* and *O. ovis*), the larvae of which parasitize nasal cavities, frontal sinuses, and the horn pedicels. Other pests of ibex are horseflies, mites, fleas *Xenopsylla,* lice *Linognathoides,* blood-sucking flies *Hippobosca* (over 500 of the latter were found in an eight-year-old ibex), and other ectoparasites (Egorov, 1955; Grunin, 1957; and others).

In the mountain systems of the Alai, Tien Shan, Altai, and Khangai, the Siberian ibex is the main carrier of itch mite *Acarus siro.* Infections by this mite have been recorded in Kirgizia and adjoining territories of Kazakhstan.[189] Instances are known of a significant number of deaths associated with this mite. The bodies of dead ibex were almost denuded of wool and their skin covered with scabs and ulcers. Moribund ibex are usually blind and highly emaciated (Dubinin, 1955; Dubinin et al., 1958). Ibex severely afflicted with scabies often descend into a valley and become the victims of predators (A.A. Sludskii). A devastating epizootic of scabies in ibex was recorded in Mongolia (1908, Khangai Aimak). It is possible that the Pamir is not free of this disease (Dubinin et al., 1958). According to Dmitriev (1938) from 1917 to 1920 Siberian ibex in the Altai died out completely at some places. Other wild animals, as well as domestic cattle and particularly sheep, died from the same disease. The symptoms described by Dmitriev leave no doubt that the disease was scabies.

---

[189] Scabies among ibex has been recorded from the Talassk Alatau in the west to the Dzhungarsk Alatau in the east (A.A. Sludskii).

Instances of ibex mortality due to starvation have been recorded during snowy winters in the Pamir, Talassk Alatau, Tersk Alatau, western Sayan, and also in Mongolia. Old males died more often than others because with their highly worn-out teeth they were incapable of chewing coarse food (Egorov, 1955; and others). A large number of ibex died during ice crust formation in the mid-1940's in Mongolia (Bannikov, 1954; Dordzhiin, 1958). In wet, cold springs mortality among young animals increases (Shul'pin, 1948).

In the Altai, Tersk Alatau, Talassk Alatau, and western Pamir, ibex mortality due to avalanches has been recorded time and again (Shul'pin, 1948; Egorov, 1955; Nasimovich, 1955). It is possible that
561 in the western Pamir during winters of excessive snow up to 10% of the ibex population dies as a result of avalanches (Egorov, 1955). In Garm district in the summer of 1949 the ibex population was seriously depleted in a catastrophic earthquake (Egorov, 1955).

An occasional cause of death of ibex is leg fractures (Egorov, 1955). Two deaths due to drowning, when the ice on the lake ibex were crossing gave way, have been noted (Meklenburtsev, 1936).

Instances of Siberian ibex sharing pastures with argali sheep, markhor, or roe deer are rare. Hence the importance of these animals as competitors of ibex is insignificant. Serious competitors are domestic goats, sheep, yaks, and horses, especially when these animals graze on the winter range of ibex in the snowfree period of the year. Indubitably domestic animals also transmit various parasitic and infectious diseases to wild goats.

In those places where there are ibex, partridges, snow cocks and marmots are also found, the alarm calls of which warn ibex of impending danger (Shnarevich, 1948; Egorov, 1955). Choughs sometimes pluck ectoparasites from the pelage of ibex while they graze or rest (Shul'pin, 1948).

A significant percentage of young Siberian ibex perish within the first few days of birth. In Aksu-Dzhabaglin preserve and the Tersk Alatau not more than 30 to 40% of all females (including juveniles not yet able to have kids) have been observed with young in summer (Shul'pin, 1948; Egorov, 1955). In the Tersk Alatau and eastern Pamir overwintered yearlings constitute no more than 13 to 16% of all the animals by spring and early summer. Egorov (1955) has characterized the summer population composition as follows (based on a count of 460 ibex older than one year in the Tersk Alatau and 603 in the eastern Pamir): females 57.5 to 59.5% and males 40.5 to 42.5% (males older than five years constituted only 9.35 to 9.80% of the total number of animals). According to Egorov there were six females capable of reproduction in the upcoming winter for every male older than five years.

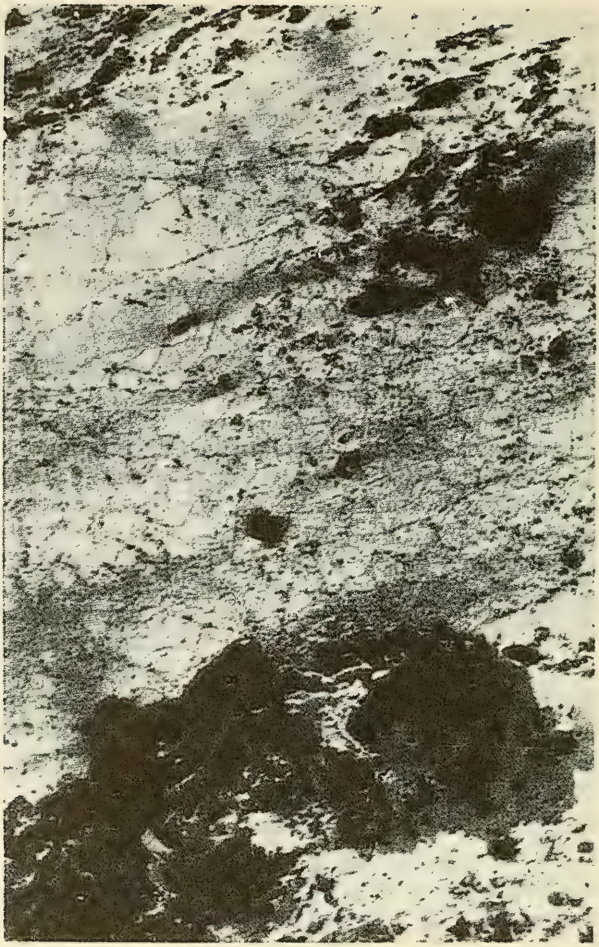
Field characteristics. Given the structure of their horns (highly compressed laterally, arced, divergent, and without spirals) Siberian ibex are not difficult to distinguish from wild sheep and markhor. 562 Females are smaller than males and have much shorter and thinner horns with poorly developed ridges. Female coloration is also more uniform than in adult males. Seasonal color dimorphism in females and similarly colored young males is relatively poorly manifested. In adult males seasonal color changes are distinct: in winter the shoulders, thighs, and chest are covered with a dark, brownish-cinnamon coat that is quite prominent against the general light dirty or yellowish-white background; summer coloration is more monochromatic (Tsalkin, 1950). In the second half of winter, due to fading and shedding of the dark-colored winter guard hair, coloration appears lighter. At the commencement of spring molt, when light underfur remains only on guard hair and intermediate hair, ibex appear almost white (Egorov, 1955).

When frightened, ibex emit a sharp whistling sound. Otherwise their voice is heard only on rare occasions, mainly before or during the period of rut. The rut bark resembles that of domestic goats but is slightly duller or hoarser.

Unlike argali sheep, frightened ibex do not run as a single herd but usually splinter into many small groups and even into individuals. Undisturbed ibex often move in single file (Egorov, 1955).

The presence of ibex can be established from their tracks, beds, and feces, which are generally similar to those of tur (see sketch), as well as from trails, clumps of light-colored winter hair clinging to bushes and rock projections, severely browsed shrubs in winter at timberline, etc.

The age of males (aided by 6-power binoculars, at a distance of up to 500 m) can be judged by counting the number of transverse ridges on the anterior surface of the horns. Usually, with the exception of the first, two ridges occur in each annual segment, very rarely one or three. The age of ibex is roughly equal to the quotient obtained by dividing the total number of ridges by two and adding one to the result. This method is not applicable for determining the age of females (Egorov, 1955). (A.N.)



561 Fig. 187. Trails and "dug up snow" of Siberian ibex. Tersk Alatau. Winter of 1948/49. Photograph by N.N. Nemnonov.

Economic Importance

Ibex are objects of hunting and sport, sought mainly for their meat. The annual catch for the Soviet Union as a whole runs probably into 10,000 to 15,000 animals and some hunters bag several dozen every year. In 1934 in Kirgizia the Soyuzkozha [hide-processing combines] received 28,480 hides of argali sheep and goats, and over 31,000 of these animals were caught (Denisov, 1935). In the 1940's hunters in Pokrov and Dzheta-Oguzov regions of the Kirgiz SSR supplied the Leskhoz Trust about four tons of ibex meat annually (Egorov, 1955).

Hunting ibex in some areas is banned, while hunting of only adult males is permitted in other areas. Hunting is by license in the RSFSR and the period of hunting restricted to a few months (autumn and part of winter).

Hunting of ibex by driving (2 to 10–30 men participate in the hunt) is common. Other methods include still hunting at places of their regular movements and near water holes; hunting by stalking is practiced less often. In Kosh-Agach Aimak of the Gorno-Altai Autonomous Region ibex are hunted with the aid of dogs which bring them "to bay" on the cliffs. When hunting by stalking, dogs are used to recover wounded animals, having been held on a short leash until then. Ibex are caught live by using nets and large traps.

Ibex were formerly taken in the Pamir by hiding behind yaks, of which ibex are not afraid, and approaching to within shooting range (Ivanov, 1885). In the Altai, Sayans, and other parts of the geographic range ibex were caught by setting up automatic shooting devices (Dmitriev, 1938).

The meat of ibex is relatively tough but tasty; in autumn up to 4.0 or 5.0 kg fat can be gathered from the viscera of large males (Egorov, 1955). The live weight of males rarely exceeds 70 to 75 kg, while females usually weigh less than 40 kg. The dressed weight of
563 meat from 40 ibex caught in the Tersk Alatau and Pamir did not exceed 47 to 51 kg in the case of males and 34 kg for females. The dressed weight represented 55 to 70% of live weight (in domestic goats, it is usually about 50%). The yield of meat from females caught in these same sections averaged 64.5% and of males 60.0% (Egorov, 1955).[190]

The hide of ibex is stronger than that of sheep and is suitable for chrome tanning; autumn and winter hides of old males are most valuable. The hides of young may be used for kid leather and the local populace convert them into wineskins for koumiss [a fermented milk drink]. Moreover, ibex hides are important in wearing apparel; people use them in making fur coats [*shuba, dokh*], outer dresses, soft shoes, and rugs.

Horns of mountain goats are converted into small articles while the stomach, after appropriate processing, is used for storage of fats, oils, and various liquids (Egorov, 1955).

Experiments on crossing male Siberian ibex with domestic goats, in particular with Kazakh and Angora goats, have been quite successful (Butarin, 1947). Crosses between wild male ibex and domestic goats have occurred evidently under natural conditions, for example, in the Pamir (Egorov, 1952). Ibex survive well in zoological gardens. Instances are known of the domestication of wild ibex by local people in the Altai (Bulavin, 1934).

---

[190] Butarin (1947) has given much lower meat yields for the northern Tien Shan: from adult males 52.5%, adult females 54.2%, and 1.5-year-old females 58.0%.

In 1949 a small group (six animals) of Siberian ibex were released in the Crimea, on the northern slopes of the Palat mountains (Chatyrdag). These goats were sighted in the first few years after their release but later not at all; obviously they perished.[191]

In view of the continuing reduction of Siberian ibex stocks, this species ought to be conserved in many parts of the geographic range; hunting should be regulated and sustained efforts made to prevent poaching.

Hunting is best permitted mainly of adult males (when their number constitutes not less than 8 to 10% of all the animals of both sexes older than one year) and restricted for one to two months before the onset of rut. (A.N.)

18. KUBAN TUR[192]

Capra (Capra) caucasica **Gueldenstaedt and Pallas, 1783**

1783. *Capra caucasica.* Güldenstaedt and Pallas. *Acta Acad. Scient. Petropolitanae,* 1779, vol. 11, p. 273. Mountains of the divide between the Malka and Baksansk on the northern slope of the Great Caucasus range, northeast of Elburz.

1888. *Capra severtzovi.* Menzbier. *Proc. Zool. Soc. London,* 1887, p. 618. Great Caucasus range, west of Elburz and south of Teberda (fixed by Lydekker, 1913). 565

1901. *Capra raddei.* Matschie. *Sitzungsber. Ges. Naturf. Freunde Ber-*

---

[191] Dal's (1958) statement that Siberian ibex survived in the Crimea and that their population reached 200 by 1954 is false. Several inaccuracies have been perpetuated by this investigator with regard to other data on Siberian ibex in the Crimea.

[192] Also called western Caucasian tur, Caucasian tur, Caucasian rock goat, or Severtsov's tur.

The local name for this species is simply "tur". All other names are artificial and bookish. "Severtsov's tur" is hardly suitable since the construction of this type of patronym is alien to the Russian language; the name "western Caucasian tur" is cumbersome. The suggested name "Kuban tur" is more convenient for usage and characterizes best the main habitat of the more typical forms of the species, i.e., the basin of the Kuban. It also differentiates this tur from the other Caucasian tur, i.e., Dagestan tur.

lin, p. 32. Upper course of Ingur, southern slope of the Great Caucasus range in Elburz region.

1905. *Capra dinniki.* Satunin. *Zool. Anz.,* vol. 29, p. 344. Western extremity of the Great Caucasus range. Suggested precise location, upper reaches of Beloe. (V.H.)

Diagnosis

Large-sized goat. Horns relatively short and massive with a broad base, and bent like a scimitar fairly steeply in a single plane. In transverse section circular-triangular in form with ridges or large wrinkles on the anterior surface. Summer beard short and winter beard fairly large. (V.H.)

Description[193]

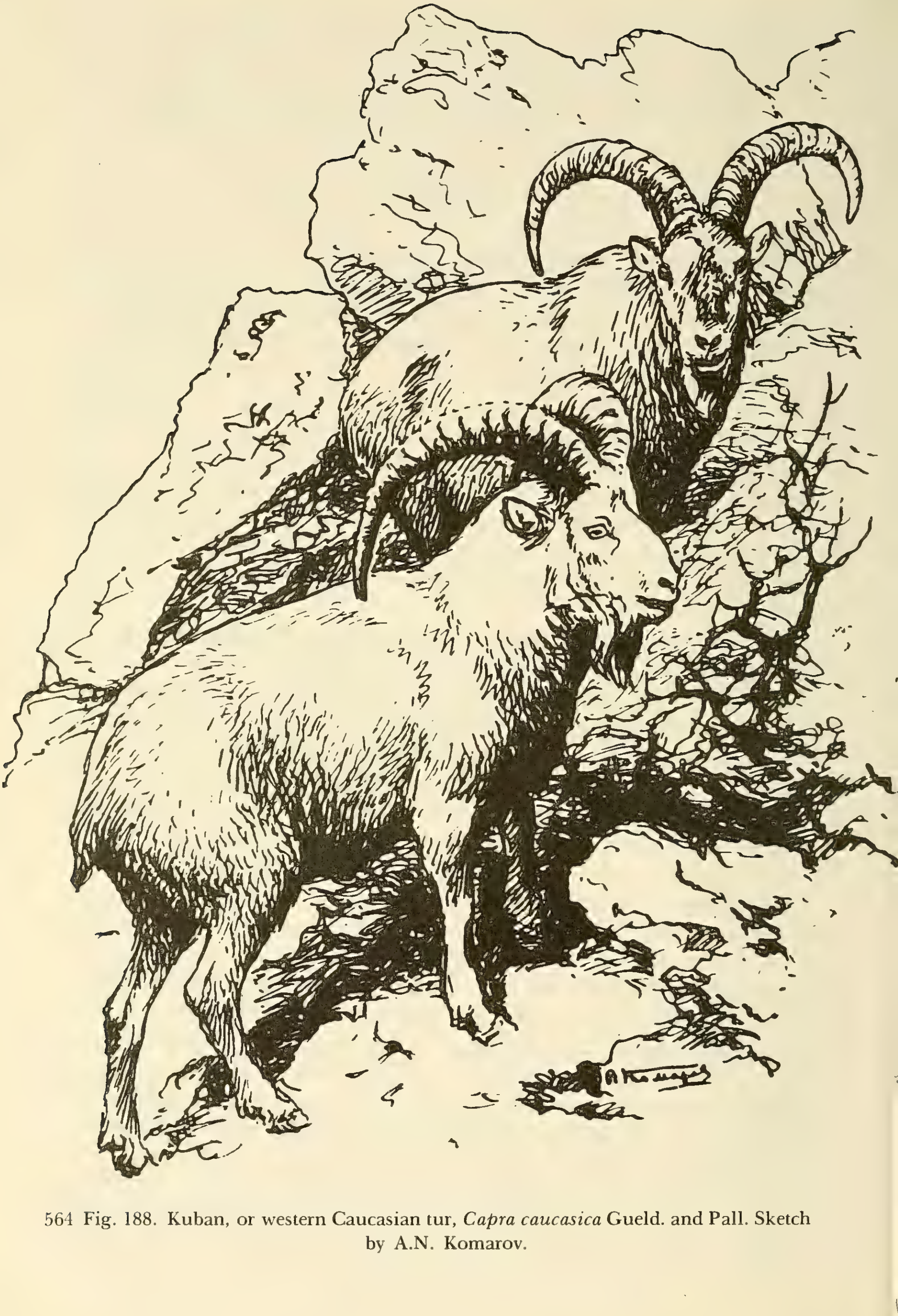
A large goat of very stout build, with a fairly massive, long trunk and relatively short but strong legs. Neck quite thick and massive, head proportionate, and ears moderate in length. On the whole the animal looks somewhat heavier and less slender than the Siberian ibex.

The horns of Kuban tur are curved and scimitar-shaped. In large individuals half or more of the horn is bent in a curve. Bending occurs in the same plane or with some deviation of the tips outward but they do not bend inward. The horns diverge sideways from the base quite strongly and their spread is generally significant. The position of the horns in relation to each other (the angle of their planes) is extremely uniform and Kuban tur do not exhibit the extreme variations seen in bearded goat or Siberian ibex.

In transverse section the horn is almost circular, or precisely, in the form of a triangle with strongly rounded angles and bulging sides, especially the anterior and inner ones; the outer side is flatter. At the very end the horn is greatly compressed laterally and rather similar to that of Siberian ibex. Only the inner ridge is well defined, the outer ridge more weakly developed, and the posterior one not discernible. In all of their characteristics the horns are fairly monotypic, but the nature of their anterior surface is highly variable. There are two main types of variations with intermediate forms between them. In one type of horn fairly high transverse prominences similar to those seen in the Siberian ibex (type "*C. dinniki*") are

---

[193] More complete information on Kuban tur has been given by Tsalkin (1955). Figures and other data given below have been taken mainly from his work.



564 Fig. 188. Kuban, or western Caucasian tur, *Capra caucasica* Gueld. and Pall. Sketch by A.N. Komarov.

clearly visible, while in the other the anterior surface has large wrinkles, which are faintly raised (type "*C. caucasica*") or somewhat intermediate between the two (type "*C. severtzovi*"). A totally smooth anterior surface is never seen.

The horns of this species are extremely massive: in relation to their length, their thickness is much greater than in Siberian ibex. In the latter the base circumference in old males is not more than 20 to 25% of the horn length. In Kuban tur, animals older than eight years with a horn length of 66 to 74 cm, have an average base circumference which varies from 28.3 to 29.0 cm, i.e., over 30%, and in some cases over 40%.

Horns of females are thin, weak and elliptical in cross section. Their curvature is slight and the whole horn bent in a single plane. Hornless animals are extremely rare.

567 "The body color of adult males in the summer coat varies on the back, flanks, and upper part of the neck from a rusty-gray to a rusty-chestnut and is sometimes fairly bright and rich. Gradually becoming lighter on the flanks, the color changes to a dirty white or yellowish-gray on the abdomen and groins. The short tail is covered on the upper surface by dark brown or brownish-cinnamon hair. On the chest and lower part of the neck the pelage is sometimes lighter than on the back, with a grayish hue.[194] The head is slightly darker than the trunk, rusty-brown on the forehead, and lighter on the cheeks. The beard is usually very short and dark or yellowish-brown.[195] On the anterior surface of the limbs a cinnamon-brown area occurs, the color intensity of which increases toward the hooves. The posterior part of the limbs is of the same color as the trunk.

"In winter the body color of adult males is grayish-brown, but is a much lighter dirty white in old animals. By spring the pelage is strongly faded and becomes even lighter. The head is darker than the trunk with a more intense brownish tinge in the forehead region. The beard is dirty brown and variable in size; in some it is short and broad and in others, long. The chest is dark, cinnamon-brown, and the belly and groins dirty yellowish-white. A dark stripe along the back is usually absent. Dark bands on the limbs are slightly fainter in winter than in summer.

"The color of females in their summer coat resembles that of males. However, the light coloration on the belly of the former is

---

[194] According to Dinnik (1910) a "dark band covered with dense, coarse, dark rusty-brown pelage occurs in the middle of the breast". (V.H.)

[195] It sometimes may attain 18 cm and is invariably longer than in Dagestan tur; the end pulled forward evidently extends to the end of the snout. Nevertheless a long beard (Bobrinskii, 1944) cannot be considered a diagnostic character. (V.H.)

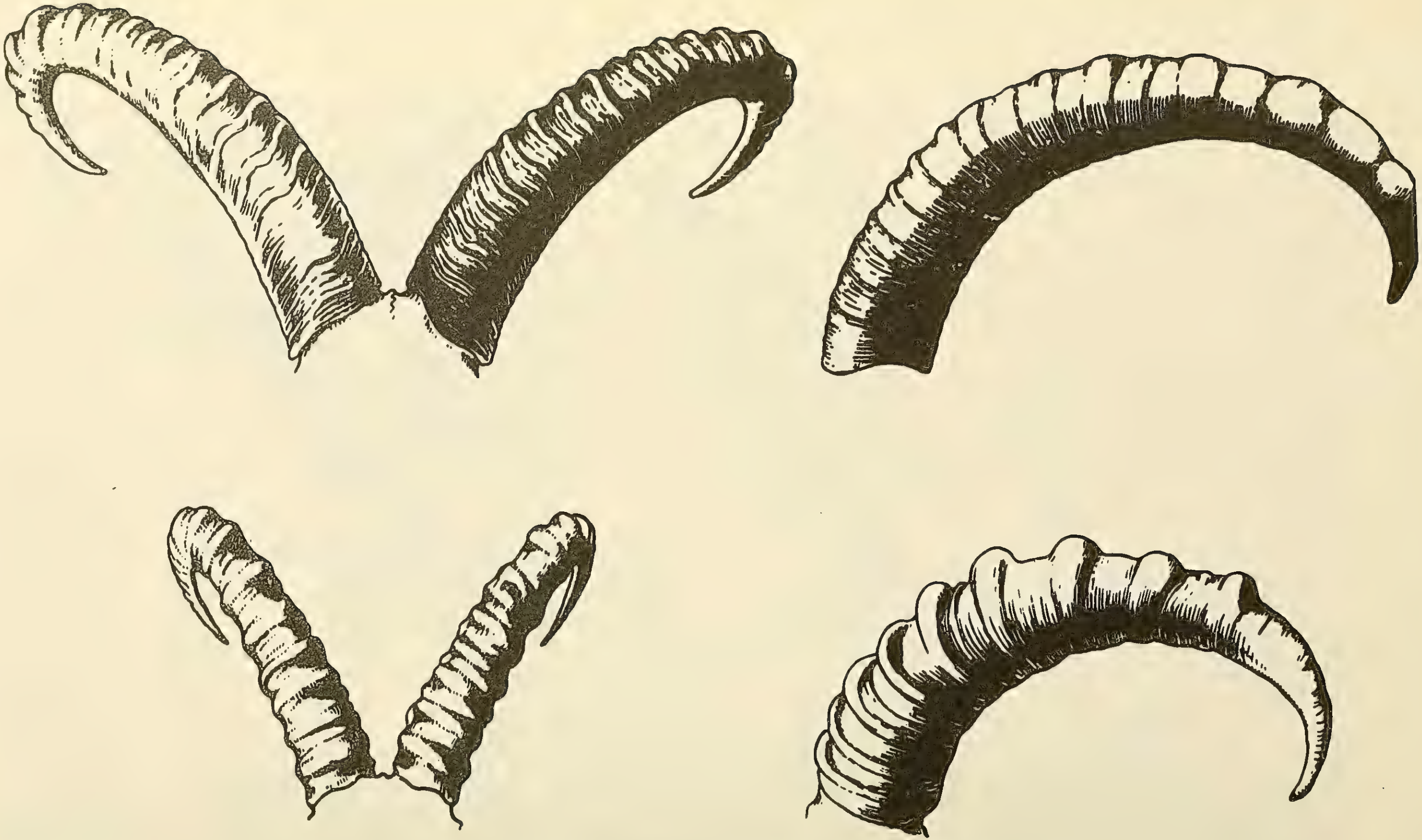
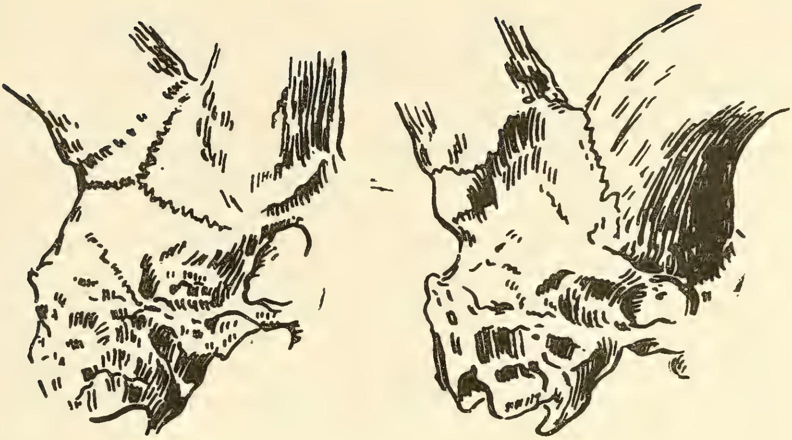


Fig. 189. Horn variations in Kuban tur, *Capra caucasica* Gueld. and Pall. Original sketch by N.N. Kondakov based on material from the Zoological Museum of Moscow University (from Tsalkin, 1955).



567 Fig. 190. Part of skull behind horns in Kuban tur, *Capra caucasica* Gueld. and Pall. (left), and Dagestan tur, *Capra cylindricornis* Blyth. Original sketch by N.N. Kondakov based on material from the Zoological Museum of Moscow University (from Tsalkin, 1955).

more vivid. Also more intense is fading on the rear of the thighs, which is less perceptible in males" (Tsalkin, 1955).

On the forehead of males the hair is long, "twisted and curly. Similar curls are also seen on the occiput, cheeks, and above the nasals, especially close to the forehead" (Dinnik, 1910).

The skull of Kuban tur is similar to that of Siberian ibex but there are several essential differences. The high point of the forehead in the former falls close to the anterior edge of the horn base; the forehead in a transverse plane is flat and in the sagittal plane con-
568 cave. The skull behind the horns is shortened and the concavity on its upper surface, i.e., on the parietals and the back of the frontals, absent. The bony horn core is relatively short and massive; in adult animals it is 30 to 40 cm long with a basal circumference of 23 to 26 cm. In transverse section it is circular and ridges are absent, although the outer surface of the core is somewhat flatter than the anterior and inner. Signs of twisting are absent. The bases of the horn core are shifted farther back than in Siberian ibex. A perpendicular line from the anterior end of the nasals to the palatal surface intersects the latter relatively close to the commencement of the tooth row, at a distance less than the length of the first three molars.

Measurements of this tur are very close to those of the Siberian ibex, and contrary to several assertions, not larger. Body length of adult males attains 150 to 165 cm and of females 120 to 140 cm; height at withers in males up to 95 to 109 cm and in females 78 to 90 cm; and height at sacrum in males as well as females slightly more than that at withers.[196] Chest circumference of males about 125 cm, tail length 10 to 14 cm, and length of ears 11 to 14 cm.

Length of horns in males 7 to 9 years old averages 66 cm, in 10-year-olds 67 cm, in 11-year-olds 69 cm, in 12-year-olds 73 cm, and in 13-year-olds 74 cm. Circumference of horn base in animals 8 years old and above averages 28 to 29 cm. Average weight of horns in animals 7 to 12 years old increases from 1.0 to 1.65 kg per year; horns heavier than 1.8 kg are a rarity. Horns of Kuban tur are shorter and relatively thicker than those of all Soviet goats and all species of the genus.

The total length of skull in males older than seven years averages 292 cm, with a maximum of 328 mm; the average length of skull in adult females is 252 mm.

The weight (data very limited) is usually 65 to 80 kg but certainly reaches 100 kg and probably even exceeds it.[197] Females are significantly lighter than males and weigh 50 to 60 kg.[198] (V.H.)

Taxonomy

The species independence of the Kuban tur is sufficiently established. In the east its range is somewhat overlapped by that of the Dagestan tur (*C. cylindricornis*) (see section "Geographic Distribution") and the two interbreed at places. Yet there is no wholly hybrid population forming a transition between these forms, i.e., the two behave as good species.

The taxonomic position of the Kuban tur among species of the genus has been poorly understood, which is the case for most remaining goats. This form is far removed from the bearded goat (*C. aegagrus*). In skull structure there are some quite distinct features of similarity with Siberian ibex (*C. sibirica*), for example, the structure of horns and horn core.

Kuban tur exhibit considerable specialization and a more progressive structure in some respects than Siberian ibex, but they are far less specialized than Dagestan tur (*C. cylindricornis*). Kuban tur might be considered a stage leading to Dagestan tur. (V.H.)

---

[196] The figures available in literature do not provide a correct idea since they pertain to rather small animals. In individual animals the proportion is invariably as given above, as for example, males 99 to 104 and 92 to 98, and females 87 to 94 and 89 to 91.

[197] Information about tur weighing up to 192 kg (Vorontsov-Vel'yaminov, 1929) is clearly an exaggeration.

[198] Some additional data, mainly craniological, are given under the description of Dagestan tur.

Geographic Distribution

Kuban tur are found in the western part of the Great Caucasus mountain range.

Geographic Range in the Soviet Union

The entire range falls within the Soviet Union, where it occupies an
569 insignificant part of the territory of the USSR. Kuban tur are confined to the high-montane region in a narrow belt along the main axis of the mountain range.

The westernmost point of distribution of this species is at Fisht and Oshten summits (2,800 m above sea level; about 39°55′ at the source of the Beloe; Dinnik, 1910). The easternmost occurrence on the northern slope is in the upper reaches of the Psygansu River (Nasimovich, 1950), a tributary of the Terek flowing from the Sugan massif. This roughly corresponds to the longitude 43°30′.[199]

The width of the range of this species, like that of the Dagestan tur, is very small, evidently much smaller than that of the latter. It varies from several to 10 to 20 km (in a straight line) and moreover nowhere exceeds 30 km. On the average it probably does not exceed 15 km. An exception is in the Elburz region where the range broadens, evidently exceeding even that of the Dagestan tur. On the southern slope it extends into Svanetiya, where it extends to the upper reaches of the Tskhenis-Tskhala and even the source of the Riona (Dinnik, 1910). Tur might reach the fairly isolated Shod massif in the upper reaches of the Riona (3,600 m above sea level), but the species is not established there. On the northern slope the range includes the towns of Kinzhal, Bermamyt, and Eshkakon, roughly 30 km north of Elburz.[200]

The range is roughly 300 to 310 km long (reconstructed range from Fisht), 15 km wide and about 4,500 km^2 in area. This is an extremely small range for a species of mammal in general and probably the smallest natural range of a large ungulate known. The Caucasian tur has the most restricted range for Soviet species of mammals.

---

[199] Assumptions (Dinnik, 1910) about the occurrence of this species of goat even farther east, in Digoria, have not been confirmed.

[200] Doubts about the accuracy of this report (Nasimovich, 1949) are hardly justified, but data on occurrence in the west at Gelendzhik (Markgraf, 1876) are probably erroneous.

Information about the residence of tur at the town of Bashtau near Mineral'nye Vody around 1800 is erroneous (Dinnik, 1910). The occurrence of tur at Kinzhal has been doubted (Dinnik, 1910). However, a specimen from this place is available in the Zoological Institute of the Academy of Sciences (N.K. Vereshchagin).

The range of the Kuban tur has shrunk somewhat in the period under review. In the 1870's tur were no longer encountered at Fisht and Oshten, but commenced only at Shugus (Chugush) summit, roughly 30 km eastward. However, at present some dispersals and brief colonization of tur are known somewhat west of Chugush (Dinnik, 1910; Nasimovich, 1949). There is no doubt that tur disappeared from some places away from the main axis of the high mountains in the south as well as in the north. Thus the animal is no longer seen at Kinzhal and its nearby summits. Information for other areas is scanty and often not sufficiently precise. Tur probably lived even in the Svanet range. At places the range contracted, though slightly, and extended along the main axis of the range beyond the widest limit shown above. For example tur lived until 1908 on the Krasnaya Polyana at Mzymta, where they are now absent (Nasimovich, 1949).

It should be emphasized that information on the range of the two species pertains to a relatively recent period. There is reason to believe that in the far remote past these ranges may have been somewhat broader, extending slightly farther east, west, and laterally from the main high-montane axis. This has been demonstrated for the region north of Elburz. Nevertheless the range even today is still quite close to the original.

In much of the range of the Kuban tur other species of goat are absent. However, in its extreme eastern part it overlaps the western extremity of the range of the Dagestan tur. The zone of overlap of the two ranges on the northern slope of the Caucasus covers the stretch between the Bezengii Cherek and Psygansu, i.e., it is about 35 to 40 km long. On the southern slope it extends from the source of the Ingur to the source of Riona, i.e., for about 50 to 60 km. Thus the overlapping region represents in the north 11 to 13% of the total extent of the range of Kuban tur and in the south up to 16 to 19%.
570 These figures are far higher than the corresponding figures for Dagestan tur.

In the southern part of the zone of overlap individuals have been seen with horns characteristic of Kuban (*C. caucasica*) and Dagestan tur (*C. cylindricornis*), and of intermediate types. Herein evidently lies the region of hybridization of the two species (Radde, 1899; Tsalkin, 1955), although there is no genuine hybrid population. When related forms come into contact with each other hybridization is natural and is often observed. It is interesting that there are not recent references to hybridization in the overlap zone on the northern slope of the range, nor to the occurrence of a hybrid population. In the western section of the area of sympatry of the two species (Bezengii Cherek) the relative population density of Kuban tur is greater than that of Dagestan tur, and less in the east (Psygansu) (Nasimovich, 1950). It can hardly be imagined that the behavior of two species in relation to each other in two parts of an essentially single region of existence would differ. Abundant material from the northern slope indicates the possibility of hybridization there also. In any case, horns apparently of hybrids have been described from this part of the range (Dinnik, 1910).

Kuban tur has been imported into Borzhomi for purposes of hybridization (see "Geographic Distribution" of Dagestan tur). (V.H.)

Geographic Variation

Geographic variation in this species with its very small range is naturally absent. The various names assigned to turs of the Malka, Baksansk, and Ingur regions (see synonyms above) and up to the western boundary of their range signify no more than individual variability of horn structure of Kuban tur.[201] The name *C. raddei* is probably based on hybrid animals.

In the westernmost parts of the range tur have long been labeled *C. severtzovi* and considered a different species from *C. caucasica.* The reason for this is that under views then prevailing *C. caucasica* denoted intermediate forms (hybrids) between Kuban and Dagestan turs (see description of latter species). Sometimes they were combined with *C. cylindricornis* as subspecies of a single species (horns of hybrids usually resemble more those of *C. cylindricornis*). It is now clear that tur from the Elburz region and "*C. severtzovi*" are identical in species relations and there are no race differences between them.

As a result of the varied interpretations of the name *caucasica,* sometimes its importance from the nomenclatural point of view is unjustly underrated. True, the description of Güldenstaedt and Pallas is imperfect and the specimens studied by them have not been preserved. However, in the region between the Malka and Baksan, whence this goat was described, neither Dagestan tur (*C. cylindricor-*

---

[201] For more details of the views which prevailed in the period when quite a few species of tur were recognized in the western half of the Caucasus, see Turkin and Satunin (1902) and Dinnik (1910).

nis) nor hybrids of Kuban and Dagestan tur have been detected. Only Kuban tur live here. Therefore it is more rational to assign the name *caucasica* to the Kuban (western Caucasian) tur as described here and as understood by other contemporary researchers (Tsalkin, 1955). In fact, however, it is better to agree that the more typical *C. caucasica* inhabits the Kuban basin, primarily the Caucasian preserve. (V.H.)

Biology

571 The biological characteristics of both species of Caucasian tur, i.e., Kuban and Dagestan, are extremely similar and essentially identical in their main features. Therefore, they have been described together under Dagestan tur.

19. DAGESTAN TUR[202]

Capra (Capra) cylindricomis Blyth, 1841

1841. *Ovis cylindricornis*. Blyth. *Proc. Zool. Soc. London,* 1840, p. 68. Eastern part of the Great Caucasus mountain range, "probably the Kazbek region" (Lydekker, 1913).

1841. *Aegoceros pallasii*. Rouiller. *Bull. Soc. Nat. Moscow,* p. 910. Nec Schinz, 1838 (Siberian ibex). Caucasus. (V.H.)

Diagnosis

A large-sized goat. Horns thick and massive, more or less circular in cross section, without knobs on anterior surface, curving gently like a spiral (back and up, in and up—heteronymous). Dark area on back absent and beard short. (V.H.)

Description[203]

The Dagestan tur is a large goat, extremely thick-set, of fairly massive build, with a slightly extended trunk, standing on low strong legs. Neck not long, fairly thick, and head proportionate, with a somewhat swollen profile (hump-nosed [Roman-nosed] . Ears moderate in length. Beard of males short and broad (see below). On the whole, the general appearance of the Dagestan tur is essentially the same or slightly heavier than the Kuban tur (*C. caucasica*). At the same time it is somewhat heavier and more massive than the Siberian ibex.

---

[202] Also eastern Caucasian tur or Dagestan rock goat.

[203] A more complete description of Dagestan tur has been given by Vereshchagin (1938) and some significant data provided by Dinnik (1910) and Tsalkin (1955).

Horns large and massive, larger and heavier than those of the Kuban tur, and unique in form. Horn initially turns up and out, later back and slightly down and in (toward the neck), and inward and up in the end portion. Thus each horn represents a very gentle, broad spiral; the right horn twists to the left and the left horn to the right (considered on the animal—a heteronymous twist). Horns at their base diverge strongly sideways, which results in a broad and gentle spread, with the ends again coming close together. The degree of curvature of the spiral, proximity of the tips, their upward flexure, the extent of the spread, and other features of horns have naturally undergone some variation. However, the general horn structure has remained extremely constant. Horn variability, especially in such features as position in relation to each other (spread), is much less than in bearded and Siberian goats. The described horn pattern is characteristic of only fully adult animals and is less distinct in young males, but the main features of horn curvature together with other horn characteristics are visible very early.

In transverse section the base and midportions of the horn are circular or slightly definable as a rounded-triangular outline. At the terminal portion the horn is compressed from the sides, the outer surface convex, and the inner flat or slightly concave. The upper and lower ridges are faint. The horn surface is fairly smooth and usually covered only with shallow transverse wavy wrinkles, which are sharper on the anterior surface. Sometimes, however, these wrinkles are rough and on the lower one-third or half of the anterior surface is even transformed into transverse knobs, often no less sharply mani-
572 fested than in the Kuban tur of the type "*severtzovi*," and exceptionally even of the type "*dinniki*". Usually wrinkles are seen in very young animals, in which this type is often encountered, but fairly distinct knobs are sometimes seen in the basal portion of horns even in animals 9 to 10 years old.[204]

The horns are thick at the base, thin slightly in the midportion, and become thinner very rapidly toward the end. On the whole, they appear thick and massive. This is particularly true of animals 7 to 10

---

[204] The view that knobs are characteristic only of animals two to six years old, disappearing later (Vereshchagin, 1938), is not fully justified.

The statement that the horn surface of Dagestan tur is totally smooth (Tsalkin, 1955) is erroneous.

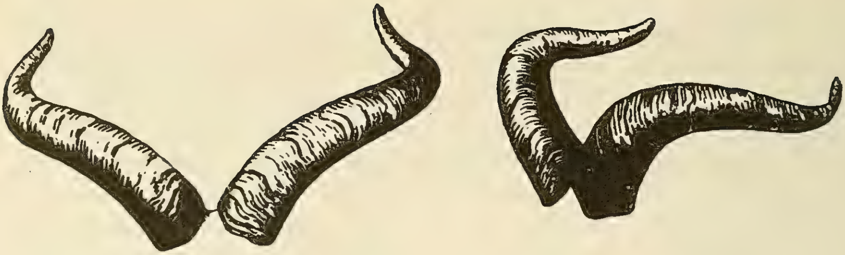


Fig. 191. Typical horn structure of Dagestan tur, *Capra cylindricornis* Blyth. Original sketch by N.N. Kondakov.

years old; horns are longer and appear slightly thinner in much older animals. The circumference of horns at the base in old animals represents about 30% of the horn length measured along the curvature, in even 50% in younger ones (four to six years). In general, however, this feature exhibits individual variability to but an insignificant extent.

Horns in females are thin and short and, at maximum growth, their length no more than 25% that of male horns; the basal circumference is 2.0 to 2.5 to 3.0 times less than in males. They are directed outward, upward, and back. They are slightly compressed from the sides, with blunt anterior and posterior ridges. Surface of horns possesses faint annular transverse elevations. Keratin is black in both males and females.

On the whole, horns of Dagestan tur are highly unique and differ sharply from those of other species of the genus. In the type of curvature there are some similarities only with the horns of the Pyrenean goat (*C. pyrenaica*). Horns of Dagestan tur are quite similar to those of some forms of mountain sheep of the species *Ovis ammon* (group *O. a. ophion*).[205]

The color of Dagestan tur is similar to that of Kuban tur. The general color of the winter coat is dark, brownish-cinnamon or chestnut-brown, and comparatively uniform throughout the body. It is slightly lighter only on the stomach, around the elbows, inside the ears, and on the lower surface of the tail. It is much darker, dark brown, on the underside of the chest and on part of the legs; it is blackish-brown or almost black on the upper part of the tail. The coat is whitish on the abdomen, inside the thighs, and on the lower portion of the tail in some animals. A faintly perceptible dark stripe runs along the back (Dinnik, 1910).

---

[205] Divergent views have existed since the time of Rul'e (1841) concerning whether the Dagestan tur represent an intermediate form between goats and sheep (Dinnik, 1910). Such views are devoid of any basis—the differences between goats and sheep are not restricted to the structure of horns alone. The Dagestan tur is a typical goat. However, other forms do show the characteristics of goats and sheep (see the description of subfamily Caprinae and genera *Capra* and *Ovis*).

The winter coat consists of coarse, stiff guard hair with a whitish proximal and brownish-cinnamon distal portion. The underfur is
573 an ashy gray color and the hair very wavy throughout its length. The average length of guard hair is 55 mm and of underfur 25 mm, i.e., the underfur is completely hidden by guard hair. The diameter of guard hair averages 182 (120 to 220) microns (upward) and the underfur about 12 (8 to 20) microns (Vereshchagin, 1950).[206]

The summer coat is a rusty-brown, cinnamon color, much lighter than the winter coat and "evidently much darker than the summer coat of turs of western Caucasus. On the posterior half of the abdomen, inside the thighs, and in the groins, it is almost white and almost the same color as in winter on the lower portions of the legs, chest, and on the tail" (Dinnik, 1910). The summer hair has an average length of 23 mm (16 to 29) and a diameter of about 153 microns (100 to 204) (Vereshchagin, 1938).

The beard of males is short and broad, usually much shorter than that of the Kuban tur. It consists of coarse hair, dark cinnamon in color, and 5.0 to 7.0 cm long. The beard commences 5.0 to 7.0 cm from the tip of the snout; pulled forward it does not reach or only just reaches the tip of the snout and does not project beyond it (compare Kuban tur). The pelage in front of the beard is short and lies close to the skin.

The skull of the Dagestan tur differs significantly from that of the Kuban tur (*C. caucasica*). In some features Dagestan tur are closer to markhor (*C. falconeri*) than to the geographically adjacent Kuban tur. This phenomenon is to a noticeable degree revealed in several points of similarity in the character of the horn curvature of Dagestan tur and markhor.

The bony horn core of the species under description is fairly long (up to 510 mm) and much longer than in the western [Kuban] tur. Moreover, it is highly twisted, corresponding to the curvature of the horns. The bases of the horn cores are broad (broader than in Kuban tur) and shifted far backward—farther than in any other species of Soviet goats. Their posterior edge projects far behind the opening of the auditory meatus. As a result of the backward shift of the horn bases the area of the skull behind the horns is extremely reduced and smaller than in other species of goats.

[206] Underfur of turs is very light and warm and greatly valued; it is used in making superior quality Caucasian hoods.

Parietals are pushed forward at an angle into the frontals and the point of juncture between the two lies in front of the line joining the posterior points of the bases of the bony horn cores, i.e., between the cores. In Kuban tur such an angle is not formed and the above point [frontoparietal] falls posterior to the line joining the posterior boundaries of the bases of the horn cores. There is a prominent concavity on the surface of the parietals and frontals behind the horns (between the posterior part of the horn bases). The high point of the skull (forehead) falls not in front of the base of the horn cores, but to the rear. The occipital crest is more weakly developed than in the Kuban tur and the cranial sutures, especially in the part directly adjoining the horns, coalesce more completely. For the remainder, the skull of Dagestan tur resembles that of Kuban tur (Figure 190).

The skull of the female Dagestan tur in all essential features is similar to that of female Kuban tur. It differs in that the horn base and the high point of the forehead are shifted posteriorly, the part of the skull behind the horns is relatively short, and the distance from the high point of the forehead to the end of the nasals is greater. These differences are essentially the same in males but more weakly expressed.[207]

In general body measurements the Dagestan tur is close to the Kuban tur (*C. caucasica*) and hardly differs from it; however, the former is generally somewhat larger. The body length of adult males is around 130, probably up to 150 cm; height of males at withers 79 to 98 cm and of females about 65 to 70 cm; height at sacrum in males 90 to 91 cm and in females about 70 cm; tail length 11.0 to 14.5 cm; and chest circumference of males behind scapula 98 to 116 cm.

The weight of males (from the fourth year and beyond) is 55 to 80
574 kg, rarely to 91–96 kg, but evidently reaching 100 or even exceeding it. Females are considerably lighter, probably to 45–55 kg or posssibly more.[208] Apparently there are no significant weight differences between the two species of Caucasian tur.

The length of horns in adult and old animals often exceeds 80 cm, sometimes 90 cm, with a maximum of 103 cm. The maximum spread of horns is 70 to 92 cm, and the distance between the horn tips in adult animals varies from 16–27 to 50–58 cm.

---

[207] The craniological features of tur are mainly from Tsalkin (1955).

[208] Published measurements of tur are few. Some of the figures given above pertain to a single animal while others refer to two or three. The same is true of weights. Weight varies greatly in different seasons. Thus, two- or three-year old turs caught in June weighed 49 and 47 kg, while an animal caught in November weighed 61.4 kg. Evidently a tur weighing 91.2 kg in August may reach 100 kg in the period of its maximum fattening. Data on size and weight are from Vereshchagin (1938 and 1947) and Dinnik (1910).

Horn measurements increase throughout life. At the age of 10 years their length is 73 to 84 cm (M 80); at 11 years 85 to 88 cm (M 86.5); 12 years 71 to 102 cm (M 84); and 13 years 73 to 103 cm (M 91). The circumference of horns at the base in animals of the same age varies (on the average) from 30.0 to 31.6 cm; the average for animals seven years old and older is 30.2 cm. The maximum weight of a single horn is 3.2 kg. On the average in animals 7 to 10 years old the weight of a single horn is 1.5 to 2.15 kg. Horns heavier than 2.0 kg in this age group and in older animals are not rare. Thus in the Dagestan tur the horn, for a given base width, is considerably longer and heavier than in the Kuban tur.

The skull length[209] in males averages 299 mm with a maximum of 310 mm. In adult females the skull length is 250 mm. In skull measurements this species is no different from Kuban tur. (V.H.)

Taxonomy

As mentioned above, there is every justification for considering Dagestan tur an independent species. It is significant that over much of its range (about one-half of it), it coexists with the bearded goat (*C. aegagrus*) without interbreeding. Over roughly 7 to 12% of its range and in 11 to 19% of the range of the Kuban tur (*C. caucasica*) the two species coexist; furthermore, interbreeding is limited and the two forms behave as good species (see below).

Among the species inhabiting the USSR, the Dagestan tur, in its characteristics, occupies quite an isolated position. It should be considered a more specialized form than the Kuban tur (*C. caucasica*). This is seen primarily in horn structure and associated skull features. It stands taxonomically farther from the Siberian ibex (*C. sibirica*) than the Kuban tur and exhibits some features relating to the markhor (*C. falconeri*). Evidently, affinities with markhor are essentially convergent in nature but nevertheless emphasize the independence of the species.

Apparently the Dagestan tur is equally isolated from species of goats outside the USSR (*C. ibex, C. nubiana,* and *C. pyrenaica*). Some features of apparent horn similarity with the Pyrenean goat (*C. pyrenaica*) are generally superficial and the differences quite significant. In the Pyrenean species the horns are set much more vertically, diverge less in the basal half, and their cross section is altogether different (dorso-inner ridge present).

---

[209] Numerical data are from Vereshchagin (1938) and Tsalkin (1955). Some differences in the values given here and those given earlier (p. 821) are explained by the heterogeneity in the material of the two species under comparison.

It is often suggested that the Dagestan tur is close to the Kuban tur (*C. caucasica*), and even that they should be merged into a single species. As noted above, the differences between the two are significant and there is every justification for treating them as individual
575 species. This is also supported by the fact that although the ranges of the two species somewhat overlap, in the region of coexistence wholly typical specimens of the two are found. Some hybrids are also seen but it is significant that a hybrid population per se is generally absent in the overlapping region (see also the section on Kuban tur).

Hybrid males of the two species bear characteristic horns which in appearance combine the characteristics of both and show an intermediate structure. It is significant that there is no special diversity in the horns of hybrid individuals and they are all comparatively monotypic. In general the horns of hybrids run initially straight back and sideways, somewhat like those of *C. caucasica,* but usually with a greater lateral spread, and later turn in and up as in the *C. cylindricornis* type. This happens in a small terminal section, which is smaller than that of typical *C. cylindricornis.* Moreover, the horns of hybrids are usually thinner and more slender than those of either species (Fig. 192). In general appearance the horns of hybrids are very similar to those of *C. cylindricornis.*

Some researchers (Dinnik, Satunin, and recently Vereshchagin, 1938) have placed hybrids under *C. caucasica,* and true *C. caucasica,* as described here, under "*C. severtzovi,*" or "*C. severtzovi*" and "*C. dinniki*". The range of "*C. caucasica*" (according to the above authors) thus coincides with the region of coexistence of the two species outlined above (see "Geographic Distribution" of Kuban tur, and below) and Svanetiya is considered the region of its principal occurrence.[210] (V.H.)

---

[210] The following question of nomenclature may arise: should we not eliminate the name *caucasica* altogether since it has been, and still is, used to designate hybrids? But the name *C. caucasica* has been used only by these authors for hybrids, foremost among them, Dinnik. What type of material Güldenstaedt and Pallas examined is difficult to conjecture now (specimens have not been preserved) but their description does not mention that they were hybrids. At the same time it is known that only one species, i.e., the Kuban (western) tur, lived at the place from where these authors obtained their material. Hence the name *C. caucasica* Gueld. and Pallas actually applies to the Kuban tur and not to hybrids and there is no justification for discarding it (see p. 825).

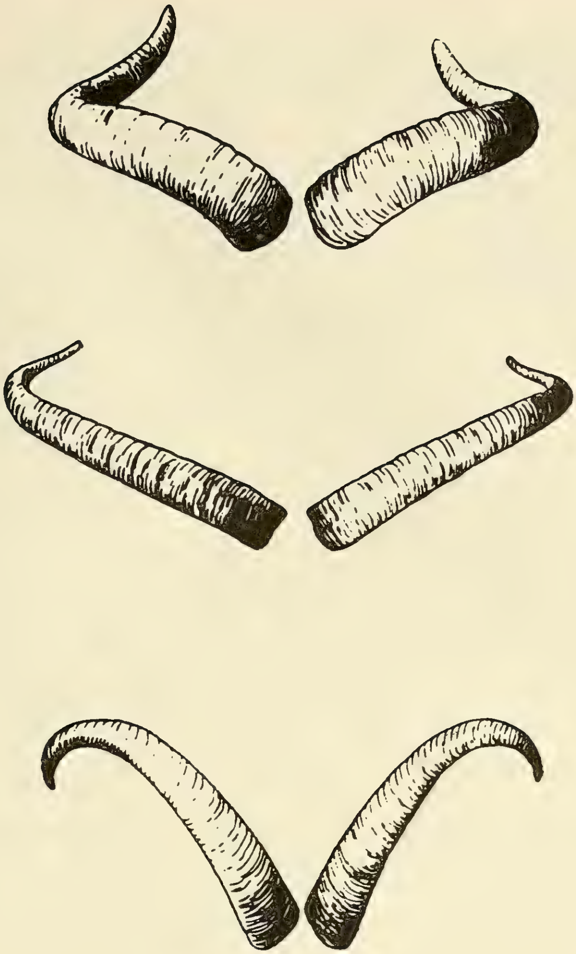


Fig. 192. Horn structure in two species of tur (upper and lower) and their hybrid (middle). From Dinnik, 1910; Vereshchagin, 1938; and other material. Original sketch by N.N. Kondakov. V.G. Heptner.

576

Geographic Distribution

The species is found in the central and eastern parts of the Great Caucasus mountain range.

Geographic Range in the Soviet Union

The entire range of the species falls within the Soviet Union. It covers a negligible part of the country's territory.[211]

The range of this tur constitutes a narrow strip extending along the high mountains of the eastern and central parts of the Great Caucasus. The easternmost point of distribution is the Gyumishli massif (2,724 m above sea level) at the source of the Pirsagat River north of Shemakha (Vereshchagin, 1938; Razevig, 1904) at 48°31′ E long., and slightly east of the Babadag massif.

The westernmost point of distribution of the Dagestan tur is the Shkhar massif, Koshtan-Tau and Dykh-Tau (Dinnik, 1910), and the source and upper reaches of the Bezengii (Khulam) Cherek (Nasimovich, 1950) bordering the northern slope of this massif on the west. This corresponds roughly to 43°05′ to 43°10′ E long.

The western limit of distribution on the southern slope of the Great Caucasus evidently corresponds fairly accurately to the position in the north. This tur lives in Svanetiya[212] and the range extends west not only to the source of the Tskhenis-Tskla but also the Ingur (Dinnik, 1910; Radde, 1899; Tsalkin, 1955).

577 Difficulties sometimes encountered in the identification of the western boundary of the range of Dagestan tur (as in the eastern boundary of the Kuban tur) are explained by the occurrence of hybrids between the two forms in the region of sympatry.

The total extent of the geographic range in a straight line from the Gyuminshli to the Bezengiisk Cherek is about 510 km.

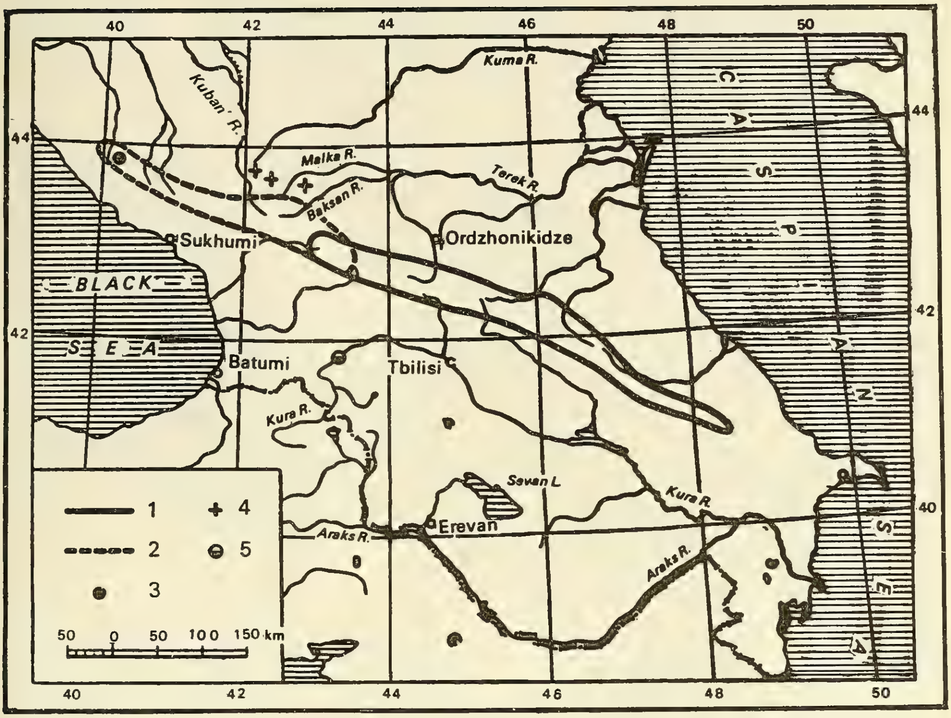
This tur inhabits the highest altitudes of the mountain range. The width of its range is not always constant but narrow everywhere and barely exceeds 30 to 35, or a maximum of 40 km, at the widest point, and is usually much narrower. For example, tur are encountered in the Kazbek massif in the midportion of the mountain range but are absent to the south at Koba and Krestovoi Pass. They are also absent to the north in Stolovaya mountain (Mat-Khokh). Here the width of the range is less than 25 km. This range slightly broadens at places where lateral spurs of the main range closely associated with its axis branch off. This is the situation in Bogossk range in Dagestan (Heptner and Formozov, 1941) where the range is apparently widest.

Evidently during the period under discussion the length of the range did not vary, or varied only slightly, although conclusive evidence for such a judgment is not available. It is, however, highly

---

[211] Additional information on this species can also be found under the description of Kuban tur.

[212] Situated in the source and the uppermost reaches of the Tskhenis-Tskla and Ingur (center, Mestiya).


40
42
44
46
48
50
44
42
40
Kuban' R.
Kuma R.
Malka R.
Terek R.
Baksan R.
C
A
S
P
I
A
N
S
E
A
BLACK
SEA
Sukhumi
Ordzhonikidze
Batumi
Tbilisi
Kura R.
Sevan L.
Kura R.
Araks R.
Erevan
Araks R.
1
2
3
4
5
50 0 50 100 150 km

576 Fig. 193. Range of Dagestan tur *Capra cylindricornis* Blyth and Kuban tur *Capra caucasica* Güeld. and Pall. (scale in km).

1—range boundaries of Dagestan tur; 2—same for Kuban tur; 3—westernmost present-day habitation of Kuban tur; 4—sites of former habitation of Kuban tur away from main axis of the Great Caucasus; 5—point of release of both species in the past (absent at present in Borzhomi). Spread of the range from east to west is shown fairly accurately, while the northern and southern limits are more or less approximate. V.G. Heptner.

possible that in the past tur were distributed somewhat farther away from the main axis of the high mountains. Thus tur existed in the Shod massif (3,600 m above sea level), at the source of Rioni, but were absent there even at the end of the last century (Dinnik, 1910).[213] In the central and eastern Caucasus there are quite a number of such sites which are quite suitable for the survival of tur but are now devoid of these animals. Such, for example, is Stolovaya mountain (Mat-Khokh) near Ordzhonikidze, situated at a height of about 3,000 m above sea level where mountain turkey [= snow cock,

---

[213] The species of tur which lived at Shod has not been established. It could even have been the Kuban tur.

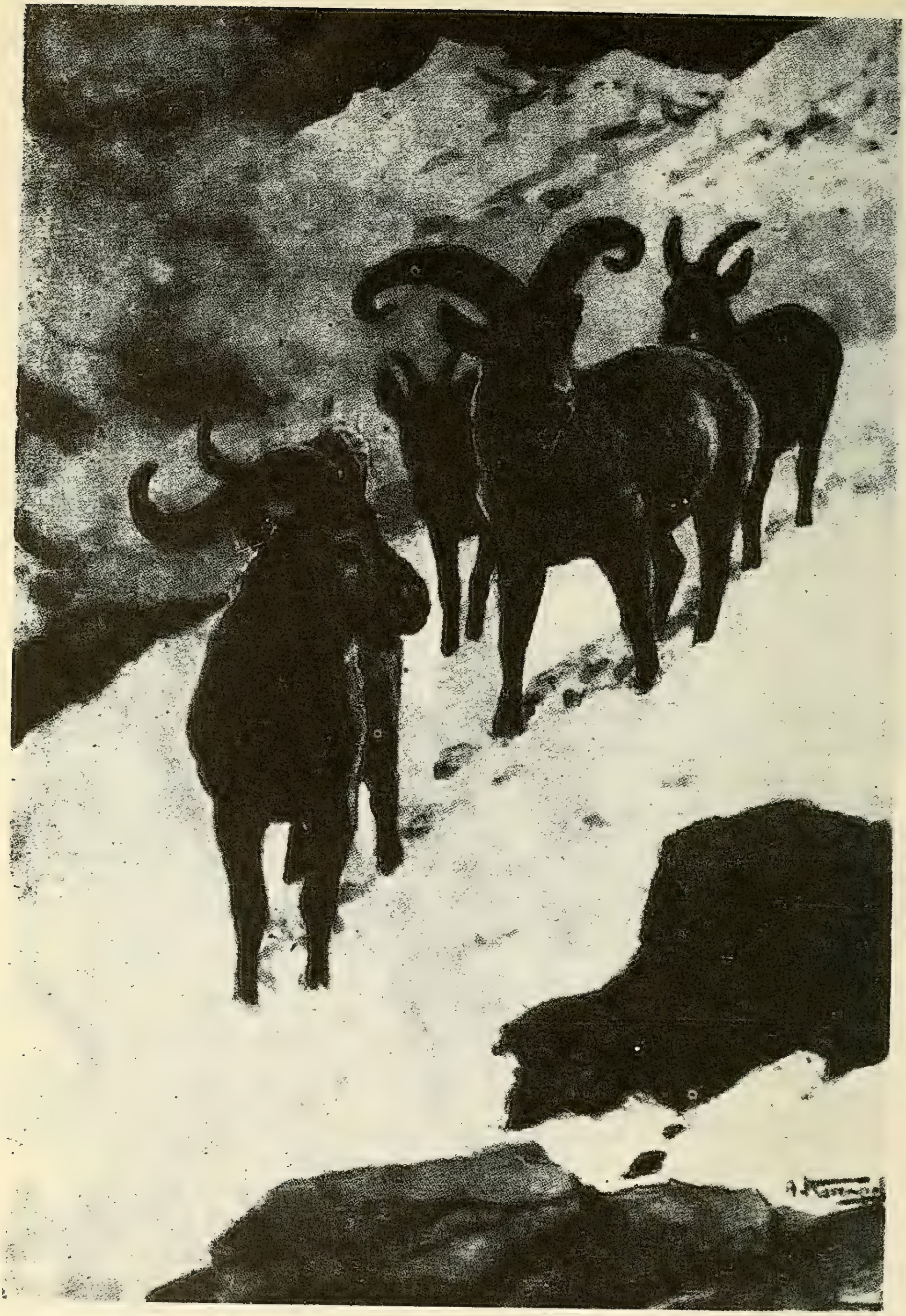


Plate 4. Dagestan tur, *Capra (Capra) cylindricornis* Blyth. Painting by A.N. Komarov.

Tetraogallus?] are present but, as far as hunters can remember, tur were absent even at the end of the last century.

Naturally, in the peripheral mountain regions, which are more accessible, more so in isolated massifs where recolonization of the animals is difficult, destruction of their population could have taken place rather easily. Furthermore, tur have been persecuted by local residents for a very long time but the collection of scientific data in the Caucasus began only some 150 years ago.

If the average width of the range of tur is taken as 25 km (more an over- than underestimation) and the length as 510 km, the total area (projected) would be roughly 13,500 km.^{2} This is an unusually small range for a relatively large hoofed animal.

The western extremity of the range of the Dagestan tur overlaps the eastern part of the range of the Kuban tur. This sympatry occurs on the northern slope in the area from the sources of the Gerek-Psygansu, flowing from Suchan massif to the Benzengii Cherek, i.e., over a stretch of about 35 to 40 km. On the southern slope this occurs in the region between the sources of the Ingur and Rioni, over a stretch of about 50 to 60 km. This region comprises 7.0 to 8.0% of the entire length of the species' range in the north and 10 to 12% in the south (see distribution of Kuban tur).

A significant part (about one-half) of the range of the Dagestan tur is overlapped by that of the bearded goat *(C. aegagrus)*. Hybridization between these two has not been observed and apparently does not occur.

Around 1888 about 20 Dagestan and Kuban turs were imported for purposes of acclimatization in the vicinity of Borzhomi (Borzhomi animal nursery). The animals survived well and reproduced, yielding many hybrids with bezoar goats which had lived there from time immemorial (Pfizenmayer, 1915). By 1917 turs numbered around 500. Shortly thereafter all the turs and bezoar goats perished (Vereshchagin, 1938).

Dagestan tur were also brought into Crimean preserve (1913) but acclimatization was unsuccessful; all of the animals were destroyed between 1917 and 1919 (Dal', 1958).

Geographic Range outside the Soviet Union

Nil. (V.H.)

578

Geographic Variation

Geographic variation has not been reported within the range and is apparently absent. (V.H.)

Biology[214]

Population. Today significant numbers of tur are found in the following preserves: Caucasian, Teberdin, Lagoda, Zakatal'sk, and in some regions reached with difficulty in the high montane region of the Caucasus (Svanetiya, Kabardino-Balkariya, and northern Ossetia). Tur are quite numerous at some places in the Azerbaidzhan mountains.

An idea of the population of tur at places where they have been well preserved may be had from the results of counts in preserves. In the mountains between the Beloe and Bol'shoi Laba Rivers in the territory of the Caucasian preserve (until around 1951), the area inhabited by tur comprised 100,000 hectares. Here in 1939 there were 6,800 tur, or an average of 70 animals (at places up to 120 to 200) per 1,000 hectares of area inhabited by them[215] (Zharkov, 1940). By the early 1950's the population of tur in that region was roughly the same.

Over 2,500 tur were counted in Teberdin preserve in 1954 and about 2,300 in 1955 (Inyakova, 1957). In 1952 the population density of tur in this preserve was close to 50 to 70 animals per 1,000 hectares of area inhabited by them (L.E. Arens).

In Zakatal'sk preserve (28,000 hectares) the area suitable for survival of tur is around 25,000 hectares. In the mid-1930's the tur population in that preserve was estimated at 4,000 (Vereshchagin, 1938), or an average of 160 animals per 1,000 hectares. At present the tur population of this preserve is probably no less. Tur are very abundant in the adjoining Lagoda preserve (13,000 hectares); 3,900 animals were reported in 1955 and even more in 1957 (K.D. Mamisashvili). 579 Although these data are apparently not entirely accurate, it is quite evident that the population density of tur here is significantly more than in the western Caucasus.

Accurate figures about the past abundance of tur are absent and their numbers can be judged only indirectly. Dinnik (1910; and others) visited many places in the Caucasus between 1877 to 1910. The largest herd of tur seen by him consisted of 33 or 34 animals (Elburz, end of the 1870's). In this same region Dinnik once sighted in a single day over 70 tur, which he says was exceptional. The mountains between the Beloe and Laba Rivers, where the Caucasian pre-

---

[214] Many biological features of the two species of Caucasian tur—Kuban and Dagestan—are extremely similar and the description here applies to both.

[215] Here and elsewhere the figures quoted are for approximately 1,000 hectares of such land usage.

578 Fig. 194. Dagestan tur in summer pasture, 2,500 m above sea level. Lagoda preserve. Photograph by A.A. Petriashvili.

serve was later instituted, were always famous for the abundance of tur. Dinnik went there many times but did not encounter herds exceeding 25 to 30 animals. Nevertheless, herds of up to 50 to 60 animals were not a great rarity in this region, and no less than 100 were sometimes seen on the horizon (Filatov, 1910; and others). From 1933 to 1937 in the Caucasian preserve, at the same places Dinnik had visited, up to 150 to 170 tur were sighted in one day; once, a herd of about 80 animals was seen. Herds of 80 to 90 animals were sighted time and again in the summers of 1946 to 1951 at the same places, while herds of 100 to 200 or more head have been reported in recent years. Encounters with large groups of tur (over 100 animals) are known in Teberdin preserve. One must consider that within the territories of the preserves of the western Caucasian mountains, the tur population at present is more than what it was 50 to 80 years ago (A.A. Nasimovich).

Radde (1899), Vitovich (1928), Vereshchagin (1938), and others have reported sighting in eastern Georgia and Azerbaidzhan tur herds containing 200 or more animals; Markov (1938) reports herds of 300 to 500 animals during the early twentieth century. In the mid-1950's the tur population in the two Trans-Caucasian preserves was very large. From 1953 to 1956 in Zakatal'sk preserve tur herds of 250 to 300 animals were sighted several times; once a herd of even 500 head was seen. In August, 1957 upto 300 tur were seen in the preserve in a single day and once a herd of 170 males was observed (A.A. Nasimovich). Encounters with large groups of tur are common even in the Lagoda preserve. Judging from all the data available, the tur population in trans-Caucasian preserves is not less than what it was in the past in these same montane regions.

Yet during the nineteenth century and in the first half of the twentieth over much of the remaining geographic range, especially in the peripheral regions of the central Caucasus, Dagestan, and in the western and in some places in the eastern Trans-Caucasus, the tur population declined significantly. This was the result not only of uncontrolled hunting, but also increased cattle ranching in the mountains and the simultaneous displacement of tur from the better pastures into areas with poor food prospects (Razevig, 1904; Endrzheevskii, 1905; Dinnik, 1910). At places along the edges to the range, for example on Achishkho mountain in the Mzymta River basin, tur were totally extinct by the early twentieth century.

Habitat. Tur live along steep rocky slopes in the mountain belt between 800 and 4,000 to 4,200 m.

In the western Caucasus, known for its humid climate and comparatively low level of permanent snowline (2,700 to 3,200 m), most tur are confined to heights of 1,500 to 3,300 m, mainly subalpine and alpine mountain belts.

The montane regions of the central and eastern Caucasus (north of the water drainage divide) have a more continental climate than the western Caucasus, as a result of which the permanent snowline runs there much higher—at 3,500 to 3,900 m. In these Caucasian regions, for example in Dagestan, in summer, when cattle are driven for grazing into high mountain pastures, many tur spend much of the day at heights of 3,500 to 4,000 m or even higher, where barren rocks, taluses, snowfields, and glaciers predominate and vegetation is extremely scanty (Heptner and Formozov, 1941; and others). Tur maintain themselves at a very high level on Elburz and in summer on Kazbek. Adult males live in sites accessible with difficulty and many are found at very high altitudes. Females and young usually live lower down the slopes.

580 In many regions some tur in summer and winter spend the entire day, or only daylight hours (in summer), on forest-covered slopes along cliffy sections. A significant number live in the forest belt of the mountains in the Kuban River basin, in Kabardino-Balkariya, Abkhaz, Dagestan, and especially in eastern Georgia and Azerbaidzhan, including the preserves, i.e., at places where they are less threat-

ened. In Zakatal'sk preserve censuses in July to early August, 1953 revealed several thousand tur; of these, 48.3% were found in alpine meadows, 29.3% at timberline in subalpine meadows, and 22.4% in the forest zone (I.F. Popkova). In regions where mountain meadows serve in summer as cattle pasture, the proportion of tur spending part of the day in the forest belt of mountains is sometimes even greater.

Food. Both species of tur are known to consume over 150 plant species, including over 100 species utilized by western Caucasian tur (Nasimovich, 1949; I.V. Zharkov) and roughly the same number consumed by Dagestan tur (Radde, 1889; Vereshchagin, 1938; Ekvtimishvili, 1953; and others).

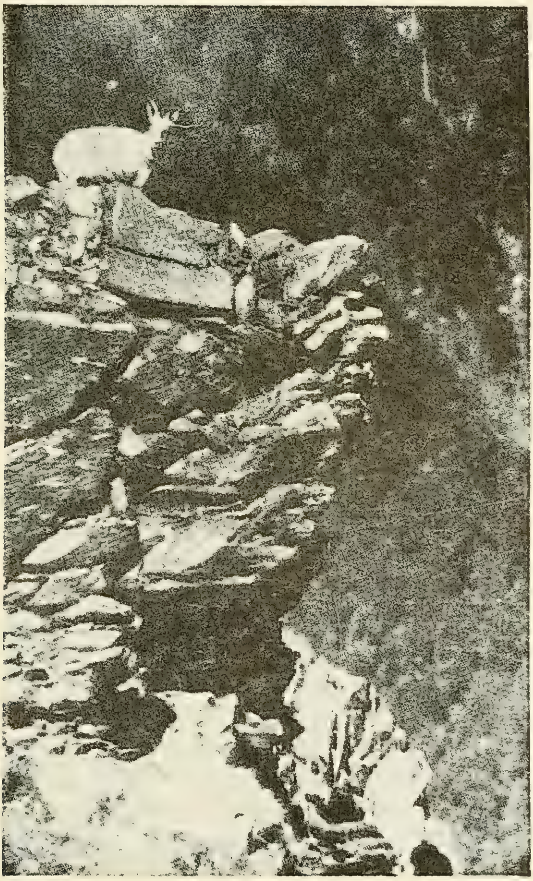


Fig. 195. Female Kuban tur. Subalpine zone of Tybgi mountains. Caucasian preserve. Photograph by N.N. Nemnonov.

In summer tur feed mainly on herbaceous vegetation (over 130 varieties). Grasses (generally up to 20 species) are well utilized as food, especially in the first half of summer; these include sweet vernal grass, foxtail, meadow grass, mountain fescue, and others. In the stomachs of seven Dagestan tur caught from June to August in the mountains of Azerbaidzhan, grasses comprised 80 to 95% by weight of stomach contents (Vereshchagin, 1938). Tur avidly consume plants of the family Compositae (camomile, cornflower, dandelion, and others), Rosaceae (bennet, meadow sweet, cinquefoil, and others), Ranunculaceae (buttercup, aconite, crowfoot, and anemone), many umbellifers, figworts (veronica and *Pedicularis*), buckwheat (Bukhara vine, sorrel), bluebell, etc. In high-montane regions close to snowfields tur feed on mountain fescue, fescue grass, sedge, gentian, and also whitlowwort *Draba,* and saxifrage (Dinnik, 1910. Lower on the slopes, where more attractive food is available, whitlowwort and saxifrage are rarely consumed. Tur bite plant stalks lower down than do chamois, sometimes almost reaching down to the roots (Fisher's cornflower and camomile), but consume only the flowers of many species, especially in the latter half of summer (Zakatal'sk preserve).

In summer tur also consume shoots and leaves of willow, birch, and other trees and shrubs; they rarely gnaw the bark of pine. In the Caucasian preserve they avidly consume mushrooms, ferreting them out in the forest. In August the stomach of a 1.5-year-old observed
581 eating mushrooms in the upper forest belt (Dzhemaruk mountain) and caught later, contained up to 1.0 kg of masticated *mlechniks* and various other mushrooms of genus *Russula.*

In winter tur feed on stalks and leaves of herbaceous plants, mainly grasses (sweet vernal grass, timothy, mountain fescue, sheep's fescue, orchard grass, crested hair grass, reed grass, and others) consuming desiccated parts as well as parts which remain green in winter. In the Kvarel'sk and Lagoda regions of the Georgian S.S.R., tur consume in winter some 15 species of forbs (8 species of Rosaceae, 3 Compositae, etc.), sedge, stalks and leaves of wortleberry, and some species of ferns (Ekvtimishvili, 1953).

Tur quite often eat standing dead-vegetation not only along windblown sections, but also from under snow cover 25 to 35 cm deep, by digging into the snow with their hooves. In sections where the snow is deeper tur eat only those parts of plants which grow above its surface (Caucasian preserve). In winter, along with herbaceous vegetation, tur consume in forests thin twigs, shoots, buds, and from time to time bark of some trees and shrubs (goat willow, birch, maple, hazelnut, pine); sometimes they also nibble at pine

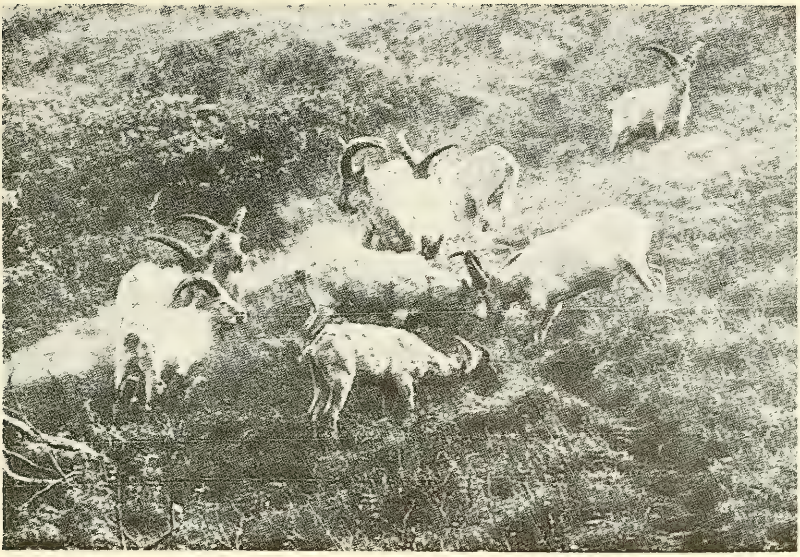


Fig. 196. Tur consuming salt scattered in an alpine pasture. Teberdin preserve. July, 1957. Photograph by G. Levenshtein.

and fir needles and are often satisfied with the hanging lichen *Usnea barbata* (Nasimovich, 1939; Ekvtimishvili, 1953). Compared to summer, tree and shrub food play an incomparably greater role in the winter diet of tur. Statements that tree bark, needles, and lichens represent an unusual food for tur (Dinnik, 1910; and others) do not agree with reality. Trans-Caucasian forests are rich in blackberry and ivy (*Hedera helix* and others). The leaves of these plants remain green in winter and serve at that time of year as one of the main foods of tur wintering in the forest (Markov and Mlokosevich, 1935; Vereshchagin, 1938; and others).

Tur regularly visit salt-licks for most of the year, including sources of sulfur. In addition, the animals often eat soil on the mountain slopes after breaking the turf first with their hooves; soil is often eaten in the upper parts of "salt licks" near the plant roots, probably because of the accumulation there of some mineral matter (microele-
582 ments) which the animal needs.[216] Near several glaciers, for example, Bezengi (Kabardino-Balkariya), tur lick significant quantities of fine particles of morainal clay. Artificial salt-licks of table salt are well visited by tur.

---

[216] F.D. Shaposhnikov's hypothesis (1953) about the physiological importance of soil intake by ungulates is not wholly convincing to the present author.

Home range. In regions where pastures and resting sites in summer occur in different sections of the mountain separated by significant distances, daily movements of a tur herd may reach 15 to 20 km. When pasturing and resting sites are close to each other, the total distance covered per day may not exceed 5.0 km. Home ranges of herds also vary equally greatly, from several square kilometers to some dozens of hectares, depending on food availability in a given area as well as other conditions. In winter, as compared to summer, animals are confined to much smaller areas.

Daily activity and behavior. In summer most tur spend the warm part of the day close to cliffs or in forests, attempting to conceal themselves in shade. Often the animals lie in beds on snowfields and glaciers close to bogs, etc., remaining there for hours. At great heights, summits of ranges, and also lower on the slopes on cool days, tur often lie in open areas. Favorite daytime haunts in the forest are ravines with mountain streams and water sources where a steady breeze occurs, which lowers the summer heat. In Zakatal'sk preserve most females with young spend almost the whole summer in such places, while males are mainly (up to 70 to 90% of all animals) found on the open slopes of alpine meadows, even in the

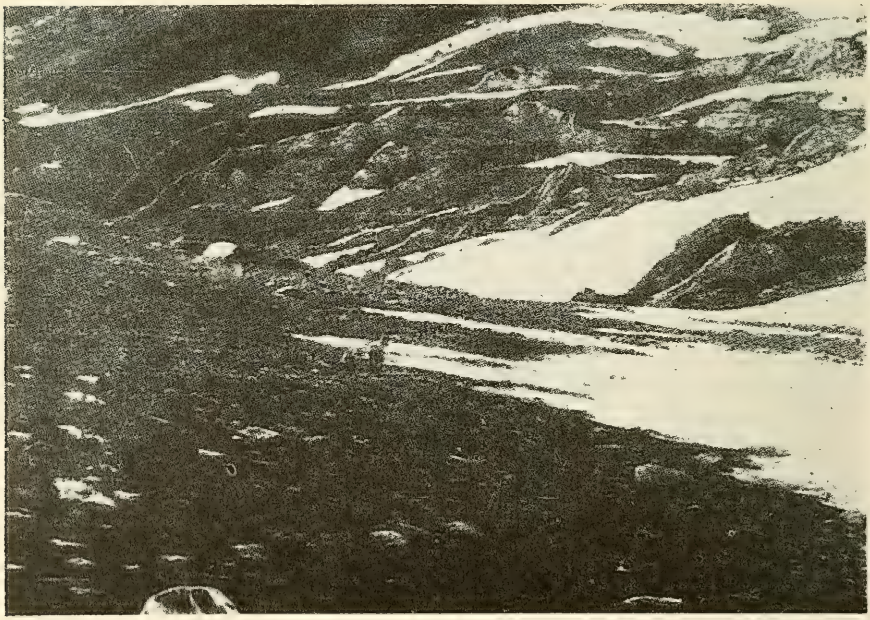


Fig. 197. Summer range of Kuban tur in Assar range. Caucasian preserve. June 24, 1952. Photograph by P.F. Kaznevskii.

morning hours (Vereshchagin, 1938; A.S. and I.P. Popkov). In August, 1957, in the Ruchug range (Zakatal'sk preserve) in the course of a single day (August 15) over 330 tur were counted in alpine meadows; of these only five were females and the rest males (adults and juveniles; A.A. Nasimovich).

In regions where tur are less disturbed, for example in preserves, evening grazing commences three to four hours before the onset of dusk. When hot weather abates they move again to open slopes of alpine meadows and grassy areas in forests. Grazing continues at intervals into the night and in the morning up to 8:00 to 10:00 a.m., after which most tur return to their beds. In cloudy weather and in rain grazing tur may be seen throughout the day.

583 Daily migration of tur is particularly distinct on the southern slope of the Great Caucasus range. There in summer the air temperature during the day in the alpine zone of the mountains sometimes exceeds 20°C and, when clouds are few, the open ground and rocks are intensely heated and horseflies appear en masse by 9:00 a.m. At that time, or even before, tur descend into forest-covered ravines or even climb up to the subnival zone (summits of the range are often cloud-capped throughout the day, while lower slopes are cloudless). If it is cool in the morning tur return to rest, unhurriedly stopping along the way to nibble grass, lingering at dry salt-licks, and traveling in 1.5 to 2.0 hours 2.0 to 3.0 km. When the morning is warm and horseflies appear early, animal movement is brisk and the same distance is covered in 15 to 20 minutes. Tur emerge again into alpine meadows only after 6:00 p.m. (August, 1957; Zakatal'sk preserve; A.A. Nasimovich and A.S. Popkov).

If cattle are grazing in alpine meadows or if tur are often threatened, they graze on open slopes only after dusk, ascending to summits at dawn or descending into forest-covered ravines. Daily vertical migrations of tur in mountains of the eastern Caucasus range from 1,500 to 2,000 m.

Yet it has been noticed in Dagestan, that in the mountains, without leaving the margins of alpine meadows, tur pass the day at the upper edge of the forest and appear in open meadows even before sundown, and regularly a few minutes after cattle have departed (V.G. Heptner).

Sometimes a herd of tur follows a fixed route in daily movement for several days (A.S. Popkov). Water holes are visited regularly only at places where summer precipitation is low and the grass dry. Tur go to water holes and salt licks only in the evening, traveling up to 10 km to reach the latter (Nasimovich, 1938).

In winter grazing and resting alternate more frequently; often the

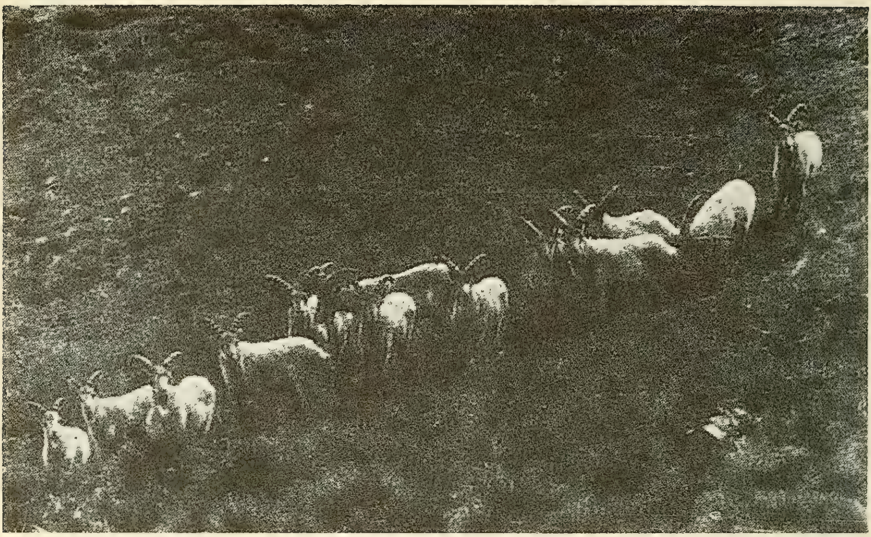


Fig. 198. Herd of male Kuban tur in alpine pastures of the Tybgi mountains. June, 1958. Photograph by V.A. Kotov.

animals remain on open slopes for the entire day, leaving them only when there is a strong wind. During continuous storms many tur seek refuge in the forest, under cliffs, and even in caves. Some animals, however, remain in their beds on open slopes even during storms, allowing themselves to be covered by snow.

584 Tur often follow the same trail. Following one another they stretch out in a long file. Generation after generation of tur apparently use fixed passages and trails in the cliffs. Rocks at such places are literally polished by the hooves of these animals. Paths through firn fields* are likewise constant. Here the trails are fairly deep troughs (Dagestan, Bogossk range: Heptner and Formozov, 1941). In powder snow over 40 cm deep animal movement is perceptibly impeded. Tur are capable of negotiating very steep slopes with great ease and ascend or descend slopes without taking advantage of projections and other uneven surfaces for footholds. Tur do not use their horns for scaling slopes,[217] and are incapable of prolonged fast running. On extremely steep slopes they often sit on their hind quarters like a dog. Such a posture is often seen in Zakatal'sk and Lagoda preserves (in Caucasian preserve slopes are more gentle and this posture rarely seen).

---

*Snowfield at the head of a glacier—Sci. Ed.

[217] Vereshchagin (1938) erred in stating that tur use their horns at difficult places to gain purchase on rocks.

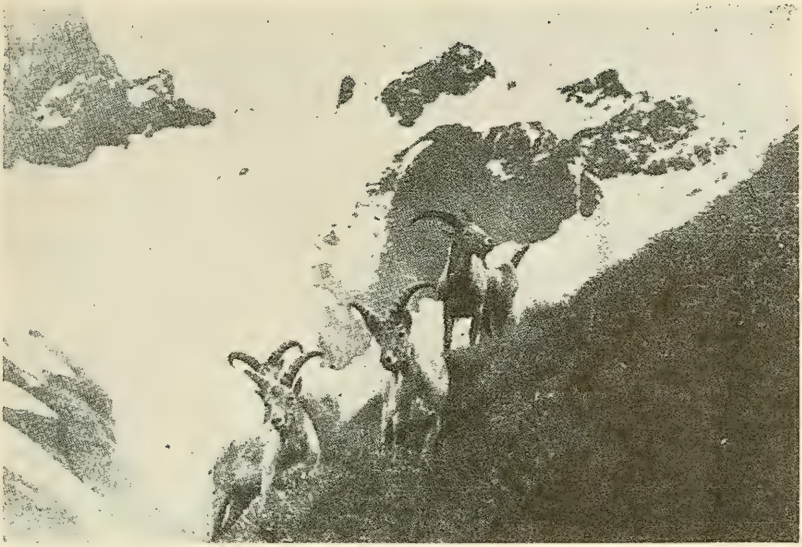


Fig. 199. Group of male tur in an alpine pasture. Teberdin preserve. July, 1957. Photograph by G. Levenshtein.

Tur often wade into water in mountain brooks and lakes. Playful tournaments among kids and even older animals (up to two to four years) are frequent in which they rear back on their hind legs and butt each other with their horns.

A herd of tur often consists of several dozen animals and exceptionally up to 500. Large herds splinter quickly into smaller groups. Herd composition is highly variable but groups of 7 to 14 animals remaining in the same herd throughout the summer have been reported (Nasimovich, 1949).

Adult males and females live separately, in independent groups, with mixed herds forming during the period of estrus and for one or two months thereafter. Juveniles up to the age of one year move with their mothers. Females up to two or three years of age move only in herds of adult females, while males of this age move in adult herds of both sexes. Sometimes animals of this age group form independent herds.

In places where tur are numerous they no doubt play a significant role in the formation of the microrelief in the alpine zone of 585 mountains. Their well-beaten trails, sometimes several kilometers long and often used for climbing, form natural terraces on slopes. Pits dug in salt licks promote the development of mounds in meadows and on fairly steep (over 35 to 40°) slopes exposed to frequent heavy showers lead to large areas devoid of a grass cover and later even to landslides. These consequences of the activity of tur are particularly prominent in Zakatal'sk preserve, where these animals are quite numerous and the terrain of the Great Caucasian range, mainly its southern slope, is extremely steep (A.A. Nasimovich).

Seasonal migrations and transgressions. In May most tur move into the alpine zone of the mountains. Females with young often spend May and all of June in the upper one-third of the forest-covered slopes and in subalpine meadows. In summer, as the snow thaws, many tur go up even higher, attracted not only by the fresh herbaceous vegetation available there, but also by the lesser number of blood-sucking insects (midges, horselfies, deerflies) and also gadflies. In many regions these migrations also depend on the grazing period of cattle in alpine pastures. In July to early August in the alpine zone of the western Caucasian mountains tur are two to three times more numerous than in the first half of June or in September. Large numbers are seen at this time of year on shaded slopes where growth of grass begins later and is maintained longer. In October grass wilts almost everywhere and then tur are often encountered on sunny as well as on shady slopes.

The first autumn snowfalls in the alpine zone compel tur living in the higher mountains to descend lower (in the western Caucasus sometimes at the very beginning of September they descend to timberline or even into the forest; Turov, 1932). This snow usually soon vanishes and the animals reascend. The final migration to the winter range occurs from the end of October to November but, at places in the alpine zone where sufficiently high snow cover forms later (central and parts of eastern Caucasus)—only at the end of November or in December. Most tur winter in the lower part of the alpine zone of the mountains (usually not above 2,500 m). In the forest they winter mostly on steep slopes with little snow, often on southern or nearly southern exposure; at some places outcrops of
586 slopes from which some snow has been blown away by wind serve as pastures. Distances traveled to reach winter range in some individual cases reach 15 to 25 km (Caucasian preserve), but mostly not more than 5 to 10 km; the range of vertical movements varies from 1,500 to 2,000 m (Nasimovich, 1955). In the second half of winter heavy snowfalls are common in the Caucasian mountains. Many tur then move into less snowy sections, sometimes descending even lower. In the upper reaches of the Khulamsk Cherek (Kabardino-Balkariya) such migrations most often occur in March (Nasimovich, 1950). In winter, and also in summer, tur usually do not descend below 800 m.

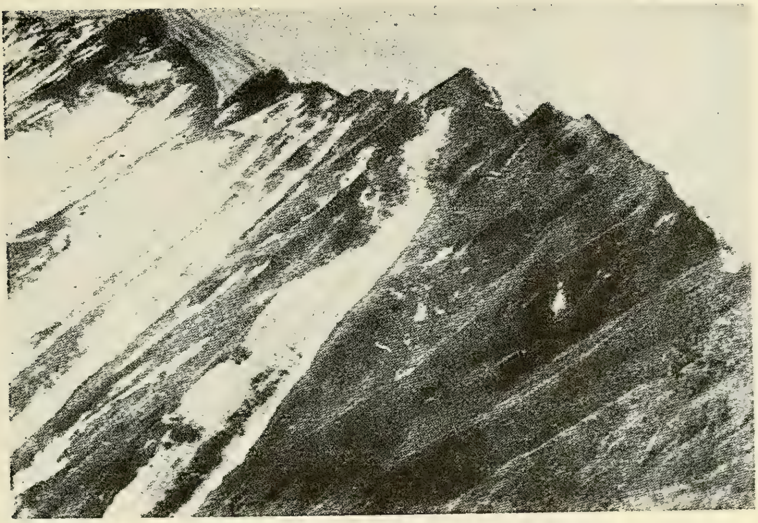


Fig. 200. Winter range of Kuban tur in the alpine zone of the Tybgi mountains. February, 1935. Photograph by G.N. Beloglazov.

In the western Caucasus several summer and autumn sightings of lone tur, or more rarely small groups, 20 to 30 km away from the sites of their permanent habitation, in mountains not more than 500 m in abs. [absolute]* altitude have been recorded. The animals disappeared from these areas later (Nasimovich, 1949).

Reproduction. Tur become sexually active from the end of November to early January, when serious combats develop among adult males. In captivity rut is more extended. In Teberdin preserve it has been detected from early November to the end of January or even in February. Gestation lasts 150 to 160 days (Inyakova, 1957). Parturition takes place in accessible sites and usually one kid, rarely two, is born. In Zakatal'sk preserve not more than 3.3 to 3.7% of all females with young had twins (Vereshchagin, 1938). Parturition extends from mid-May to around June 20 in nature and in captivity up to mid-July. In Caucasian preserve the first newborns are not seen before May 17; most are seen from the end of May to early June (Nasimovich, 1949). Mass births also occur in Teberdin (N.M. Malinko) and Zakatal'sk (Vereshchagin, 1938) preserves during this period.

Sexual maturity is apparently achieved in tur in their second year but many females that age are not sexually active. Young males,

---

*This appears to be contrasted "relief" of 500 m.—Sci. Ed.

Fig. 201. Herd of male Dagestan tur crossing a spur of the Ruchug range. Subalpine zone of Zakatal'sk preserve. February, 1958. Photography by A.S. Popkov.

inferior to older ones in strength, take part in reproduction only in their fourth or fifth year. A fairly large number of adult females remain barren every year. In captivity females reproduce every year (Dzhanashvili, 1943).

Growth, development, and molt. Kids remain helpless for only the first few hours after birth. On the second day it is difficult to catch one even in a small enclosure (Inyakova, 1957); from that time 587 the young follow their mothers who live a secluded life for ten days after parturition. At the age of one month kids begin to eat grass. Suckling continues until the end of summer, in rare cases even longer. Lactating females have even been captured at the end of autumn and winter and encounters with two-year-old suckling females who had probably lost their kids in that year have been noted (Nasimovich, 1949; and others). In the Tbilisi Zoological Garden female tur yielded in June 635 to 900 g, average of 810 g, milk per day (Vereshchagin, 1938).

A newborn tur kid weighs 3,500 to 4,200 g. In Teberdin nursery (N.M. Malinka, A.P. Inyakova, and others) the weight increase of two kids caught in spring was as follows (in kg):

	First year	Second year		Third year		Fourth year
	October	April	October	April	October	April
Male	19.5	27.0	46.0	52.0	68.0	74.5
Female	21.5	25.5	39.0	38.0	51.5	61.5

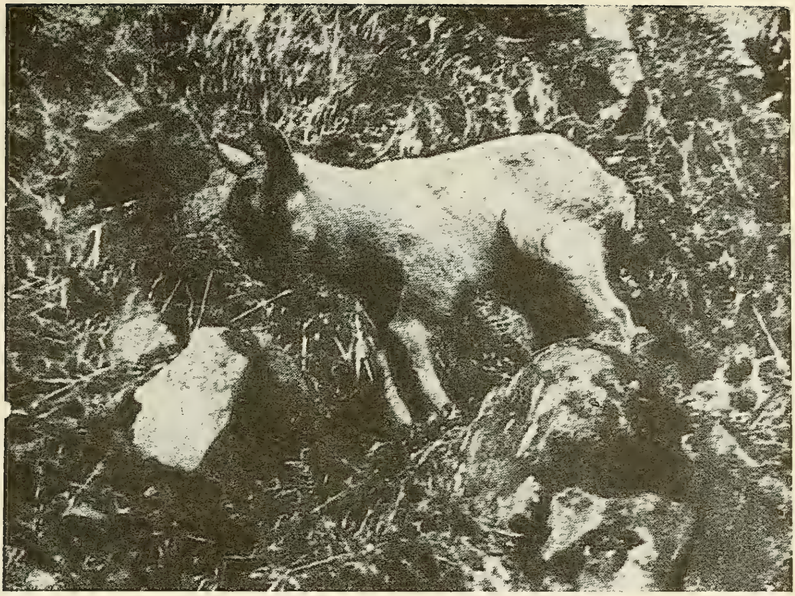


Fig. 202. Tur kid one or two days old. Atamazhi mountain. Caucasian preserve. May, 1941. Photograph by I.V. Zharkov.

Under natural conditions young tur gain almost no weight in winter while adults usually lose weight. The live weight of adult male tur is 65 to 80 kg, rarely as much as 100 kg, and of females 50 to 60 kg. There are no significant differences in body measurements between western and eastern Caucasian turs (Tsalkin, 1955).

In Teberdin nursery (1,300 m abs. elevation) molt of juveniles commences from the end of June to early July and ceases by the end of August. After this the gray tone almost disappears from the pelage, which turns cinnamon. The winter coat develops in juveniles from mid-September through mid-October (N.M. Malinko).

Development and shedding of teeth has been studied very little (Vereshchagin, 1938). Horn growth in kids commences from the first week of birth. In winter in nurseries keratin formation slows down but does not stop (N.M. Malinko). The horn circumference at the base usually increases for up to 8 years, more rarely up to 10 to 11 years (Tsalkin, 1955). In eastern Caucasian tur the maximum increase in horn mass has been recorded for animals six to eight years old (Vereshchagin, 1938).

588 The maximum sexual activity has also been recorded for animals six to eight years old. Longevity of tur is not precisely known but under natural conditions most evidently die before the age of 10 to

12 years, rarely surviving for 15 to 16. Vereshchagin (1938) thought that some tur lived for as many as 22 years.

Adult tur molt from March to mid-June or early July. In the western Caucasus some lone adult males retain patches of old winter fur in the sacral region even at the end of July. In Autumn the guard hair of adults begins to grow perceptibly from September[218] and underfur appears in this same period; the winter coat is complete by the end of October (western Caucasus, Dagestan) or middle of November (Alazan River basin) (Vereshchagin, 1938; Nasimovich, 1949).

Enemies, diseases, parasites, mortality, competitors, and population dynamics. Enemies of tur are leopard, wolf, and lynx, but the first-named predator is now very rare in the Caucasus. Tur remains have been seen in 12% of feces of wolves collected in Caucasian preserve in different seasons of the year (Teplov, 1938). The Abkhazian names for tur, i.e., "abg-ab" and "abg-adzhma" (wolf billy and nanny), originated, no doubt, from frequent instances of persecution of tur by wolves.

Tur remains were found in 19.1% of the 136 lynx stomach contents analyzed in recent years in Caucasian preserve; these remains were maximum in the winter–spring period—26% (Kotov, 1958). In the event of an unsuccessful attack on tur (lynx usually attack from ambush), the predator does not attempt to pursue its quarry and the tur does not run far away (I.V. Zharkov). Reliable reports of successful attacks on tur by bear, golden eagle, and lammergeier are unknown to us.

The diseases of tur have been studied very little. At the end of the nineteenth century an unidentified epizootic disease ended in mass mortality of tur in the eastern Caucasus (Mlokosevich, 1894). In the first quarter of the twentieth century in the western Caucasus, cattle suffered from a plague which affected wild ungulates, including tur
589 (Nasimovich, 1949). Tur contract hoof-and-mouth disease from domestic animals. In the Tybgi (Beloe River Basin) in the summer of 1898 a large group of lame tur was sighted (Shil'der, 1901). In zoological gardens mortality of tur due to necrobacillosis has been recorded.

Scabies, evidently caused by the mite *Acarus siro* (Dubinin, 1955), was reported in 1932 and 1933 in tur in the eastern Caucasus (Vereshchagin, 1958). In some tur large areas of skin were denuded of pelage. Tur with symptoms of a similar disease (sometimes sev-

---

[218] In 1957 in Zakatal'sk preserve some adult males began acquiring a very dark color, transitional to that of winter, even in mid-August.

588 Fig. 203. Females with young kids. Dzhalovchat glacier region at the foot of the Aksaut massif. Western Caucasus. End of July, 1958. Photograph by G.L. Levenshtein.

eral animals in a herd were definitely sickly) were sighted in Lagoda and Zakatal'sk preserves even in subsequent years. Unfortunately the subject of scabies in tur has not been investigated to date.

An adult tur caught in Uchkulan gorge near Teberdin preserve died within a month from coenurosis (Ekvtimishvili, 1952). Similar diseases have been recorded for Dagestan tur (Z.S. Ekvtimishvili). In Caucasian preserve nine species of helminths have been identified (including seven species of nematodes). Intensity of infection reached as much as 1,390 helminths per animal (D.P. Rukhlyadev).

Tur suffer from nasopharyngeal gadflies (*Oestrus caucasicus*[219] and *O. ovis*) (Grunin, 1957). Hair lice and mites have been detected in dead animals (Vereshchagin, 1938). Periodically they suffer severely from horseflies, and also deerflies, midges, and other bloodsucking insects.

Tur mortality due to snow avalanches has been recorded in the basins of the Beloe, Laba, Aksaut, Teberda, Baksan, Cherek, and Alazan Rivers, the Bogossk range in Dagestan, etc. (Dinnik, 1884 and 1910; Vereshchagin, 1938; Nasimovich, 1939; Heptner and For-

---

[219] Vereshchagin (1938) mistook the larvae of this species for *Hypoderma bovis* (Grunin, 1957).

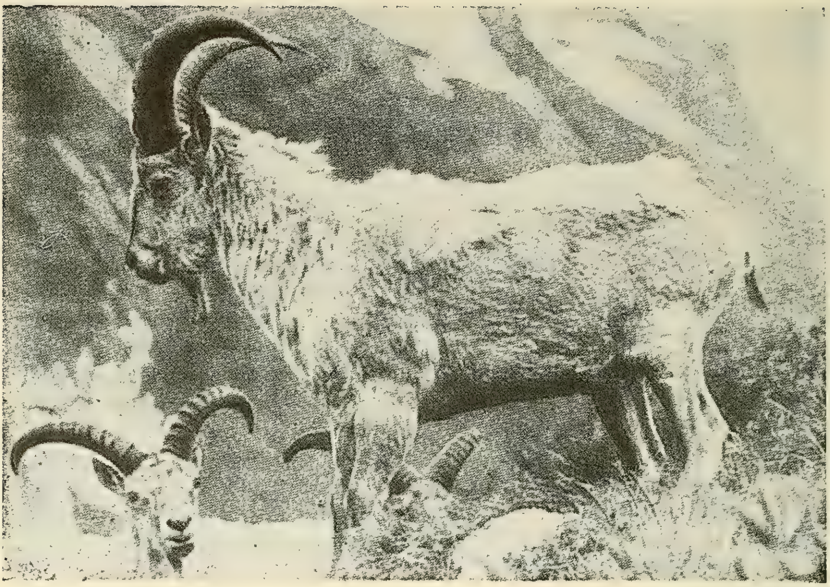


Fig. 204. A molting adult male Kuban tur. Teberdin preserve. End of July, 1957. Photograph by G. Levenshtein.

mozov, 1941; Arens, 1957; and others). In Zakatal'sk preserve tur remains are found almost every year at places of thawed avalanches. In particularly snowy winters tur find it difficult to obtain food and
590 to move over deep, soft snow. In such winters even adult males can be overtaken by a man on skis (Caucasian preserve). Instances are none too rare of tur mortality due to rock formations giving way (Zakatal'sk preserve). Deaths of adult and young tur due to falls from cliffs have also been reported (Caucasian and Zakatal'sk preserve).

The most serious competitors of tur for grazing in mountain pastures are domestic livestock, and particularly sheep and goats. The development of animal husbandry, no less than persecution by man, has driven these wild ungulates into less suitable montane habitations, resulting in a perceptible reduction of tur population. The chamois is also a competitor of tur. In summer 50% of chamois food consists of exactly the same species of herbaceous plants as are consumed by tur. In winter tur and chamois are usually confined to different montane regions (see section "Biology" under chamois for competitive relations between tur and chamois). Dagestan and western Caucasian turs when held together interbreed, but in nature this seldom happens. In zoological gardens and under conditions of semifree living (near Borzhomi) tur interbreed with bearded goats, but again hybrids are exceptionally rare in nature (Pfizenmayer, 1915).

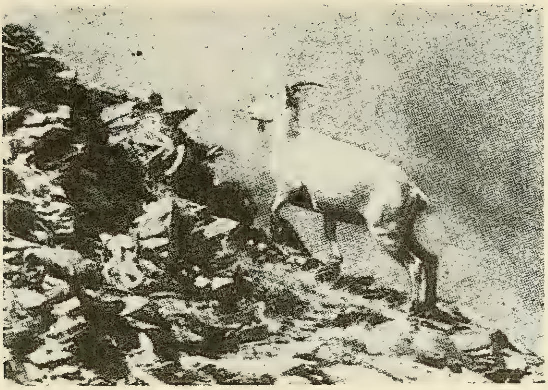


Fig. 205. Female Kuban tur. Tybgi mountain. Photograph by N.N. Nemnonov.

In the Great Caucasus the distribution of the mountain turkey (= snow cock, *Tetraogallus*) coincides closely with the habitat of tur in the alpine zone. After heavy snowfall snow cocks utilize the pits dug by tur, searching there for food.

Significant fluctuations in tur population due to natural causes, unrelated to human intervention, are rare. The population composition of tur has not been well studied. Evidently a large number of kids die in the first few days after birth. In summer in Zakatal'sk preserve and adjoining regions only 34 to 37% of adult females bore kids (Vereshchagin, 1938). In the alpine zone of Caucasian preserve from July through September (1927 to 1937) kids born in the previous spring comprised 15% of the entire tur population (Nasimovich, 1949). Similar figures have been given by Zharkov (1940) for the summer of 1939.

In tur herds encountered in alpine meadows of Caucasian preserve the sex ratio among adult animals was close to 1 : 1, but females were predominant in the forest (60 to 84%) (Nasimovich, 1949). In the 1939 census of those animals in which the sex was determined, 1,192 were males and 827 females (Zharkov, 1940), i.e., the ratio of males to females was close to 3 : 2.

In Zakatal'sk preserve, especially in the higher mountains, encounters with males significantly predominate. In the 1956 census the sex of several thousand adult tur living mainly above timberline was established and males comprised over 80% of the population (A.S. and I.F. Popkov). Such a sex ratio can only be explained by the more secluded life style of females, which spend much of the summer in the forest belt or migrate into other regions (the latter alternative is less probable).

Field characteristics. In the Caucasus tur, chamois, and bearded goats are seen in the same habitat. Tur differ from chamois not only in their massive build, large horns, and less vivid chestnut summer 591 coat without black coloration on the abdomen and legs (typical of chamois), but also by their sharp and intermittent whistling, so unlike the continuous hiss emitted by chamois.

Tracks of tur are larger and much broader than those of chamois. In tur the anterior part of the print is blunt but in chamois quite sharp. The outer lateral margin of the hoof of tur has only an insignificant bulge.

The presence of tur can be established from well-beaten trail across slopes and feces in the form of pellets that are slightly larger than those of domestic goats and chamois. Often tur feces consist almost wholly of fine clay swallowed during visits to salt licks. Molted tufts of tur wool can be seen in winter on rocks and shrubs, which by spring have bleached and appear white.

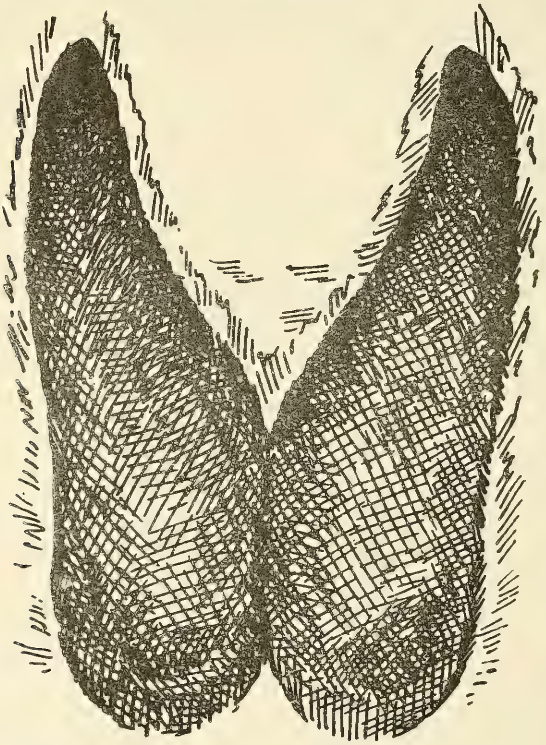


Fig. 206. Hoofprint of male Kuban tur on wet argillaceous soil (normal size) Caucasian preserve. Sketch by A.A. Nasimovich.

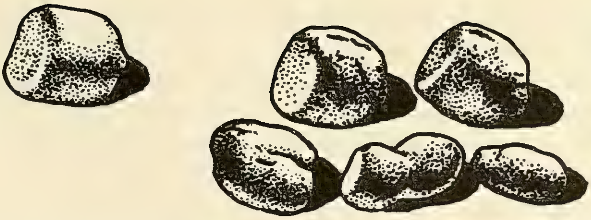


Fig. 207. Feces of tur (natural size) after consumption of soil in a dry solonetz. Upper reaches of Bezengiisk Cherek. Balkar. September, 1949. Sketch by T.L. Savranskaya.

At places where tur are numerous evidence of their grazing in meadows cannot be missed; a characteristic "goaty" smell often hangs in the air. The clatter of horns of fighting tur can be heard from a distance of 2.0 to 3.0 km.

Tur are fond of resting on slopes covered with sparse vegetation, or even on those that are totally devoid of it, and in sections covered with fine rubble, clay, or talus; small ledges on cliffs are particularly favored.

Male tur are appreciably larger than females and have much longer and more massive horns; in old males the horns reach 75 to 81 cm in length (Kuban tur) or even 100 cm (Dagestan tur) with a base circumference of 27 to 35 cm. Horns in females rarely exceed 30 cm in length with a base circumference of slightly over 10 cm (Dinnik, 1910; Tsalkin, 1955). Moreover, horns of males have a more complex curvature, which is particularly characteristic of Dagestan tur. In males the "beard" is well developed.

592 Economic Importance

Tur serve as an object of sport and partly of commercial hunting. The maximum number of animals are hunted by residents of high-altitude villages, especially shepherds. The overall annual harvest in the Caucasus totals some thousands of animals. For the mid-1930's the annual harvest of tur in Azerbaidzhan and adjoining sections of Dagestan was estimated at 2,850 animals (Vereshchagin, 1938).

Hunting of adult males only is permitted and licenses required. In 1953 the hunting season in Azerbaidzhan extended from July 15 through November 1 (in 1956, through December 1), in Dagestan from September 1 through November 1, and in Kabardino from September 1 through December 31. In that same year (1953) hunting of tur was banned in the Georgian S.S.R., Northern Ossetian Autonomous S.S.R., and Stavropol' and Krasnodar territories. In 1957 hunting of tur was banned in the Georgian S.S.R. and some other regions of the Caucasus.

Most tur are hunted by shooting from ambush at places of their regular visits, near salt licks, and so on. Group hunting by chasing is also practiced, utilizing dogs in summer and autumn in Dagestan (Heptner and Formozov, 1941). In the 1860's winter parties of up to 50 mountaineers on skis caught in a single day up to 30 tur near Latsuri glacier (Tskhenis-Tskla River basin, western Caucasus) (Radde, 1866). Catching tur in traps and snares, often practiced in the past, is now banned.

An adult male tur yields 40 to 55 kg of dressed meat of excellent taste. An adult Dagestan male tur weighing 61 kg and caught in November before rut when the animals are fattest, yielded 60% of total weight in meat, 4% in liver, kidneys, and other viscera used as human food, 17% in head, legs, and hide, and 19% as stomach and intestines with their contents. A three-year-old tur caught in autumn yielded 2.0 kg of fat (Vereshchagin, 1938 and 1947; and others).

Tur hides are used, or at least were in the past, for bedding, indigenous soft shoes (pumps), wineskins, covers for saddles, household straps, and chamois. Winter hides with the guard hair plucked out were used in making warm jackets and *papakhas* (tall Caucasian hats made of skin) and light and warm hoods made from winter underfur (an adult tur yields up to 350 g of underfur). Horns are presently used as wall decorations; in the past they were used in making various articles such as handles for knives and daggers, ladles, and so on. Silver-covered horns were used in Georgia for drinking wine during solemn feasts. Horns of adult males weigh 5.0 kg (Vereshchagin, 1947).

Tur caught young and taken care of live well in captivity and may interbreed with domestic goats, which has happened in mountain villages (Endrzheevskii, 1905). In the 1930's experiments on crossbreeding Dagestan male tur with domestic goats were conducted in the Tbilisi Zoological Garden. Fertile hybrids were larger in size (up to 120 kg) than the original parental stock. The milk of these hybrids is characterized by a high fat content (5.5 to 6.0%) and the daily milk yield is one to two liters (Dzhanashvili, 1943; and others). The weight of a three-year-old hybrid "turgoat" (I.F. Salymov; Krasnopolyansk region of Krasnodar territory) in summer reached 107 kg, almost twice that of domestic goats of the same age. Hybrid males of the first generation become sexually mature 16 months after birth, while hybrids of the second generation (25% tur blood) do so after 8 months (A.G. Bannikov). Experiments on the artificial insemination of sheep with tur sperm (Teberdin preserve) predictably were unsuccessful (Lopyrin et al., 1956).

From 1888 to 1890 many tur were brought from Svanetiya and the Kazbek regions and placed in a special enclosure (fenced section) near Borzhomi on the spurs of the Akhaltsikho-Imeretinsk range (Pfizenmayer, 1915). Here tur acclimatized well and multiplied; the fence was later partially removed and the animals began to wander widely. In 1917 there were about 500 tur and herds of up to 50 animals were sighted (Vereshchagin, 1938). Sad to say these tur were
593 completely destroyed over the next few years. In 1913 Dagestan tur were brought into the montane parts of the Crimea, initially held in a pen, and later released only to perish subsequently.

In most regions tur need to be conserved, but this has not yet been well organized since the control of hunting of these animals in the mountains is fraught with many difficulties, and grazing of domestic livestock in montane pastures has only recently been adequately regulated. In regions where hunting of tur is permitted it is desirable to restrict it to from early September through the end of October or November. Acclimatization is possible south of the Great Caucasus, for example in Nagornyi Karabakh (Vereshchagin, 1938), and also in some other regions of the country. (A.N.)

20. SCREW-HORNED GOAT OR MARKHOR[220]

Capra (Orthaegoceros) falconeri Wagner, 1839

1839. *Aegoceros (Capra) falconeri.* Wagner. *Munchn. Gelehrt. Anz.,* vol. 9, p. 430. Kashmir and Astor.

1945. *Capra falconeri heptneri.* Zalkin. Tsalkin. *Doklady Akademii Nauk SSSR,* vol. 46, no. 5, p. 231. Dashtidzhum region of Tadzhikistan.

1945. *Capra falconeri ognevi.* Zalkin. Tsalkin. *Doklady Akademii Nauk SSSR,* vol. 46, no. 5, p. 232. Kugitangtau mountains, Karlyuk region of Turkmenian S.S.R. (V.H.)

Diagnosis

Large-sized goats. Horns long, compressed from sides, with a sharp anterior ridge, without knobs, and twisted into a steep heteronymous spiral. Males in winter coat sport long hair on neck and a large tress below the neck; beard large. (V.H.)

---

[220] The first is a bookish, artificial name and the latter, a local name used in Kashmir which has entered English and Soviet literature. "Mar" means snake.

Description

The markhor, in general form, is a strong animal of stout build but slightly lighter than the Caucasian tur. Trunk not as greatly elongated and legs slightly longer, but powerful and fairly thick. Head proportionate with a bulging nasal region (hump-nosed), and a slightly concave forehead. Neck, due to intense overgrowth of hair (see below), appears very thick and massive, especially in winter coat. Hooves thick and short.

Horns of males large, long, massive, and twisted in the form of a typical spiral ("screw" or "corkscrew"). Spiral quite variable in curvature, but invariably heteronymous (left horn of animal has a right-handed twist and right horn a left-handed twist) and general axis of all turns (i.e., the horn as a whole) invariably straight. Number of turns of spiral up to 2.0, 2.5, or even 3.0. In younger animals spiral gentler and circumference wider; in old animals spiral tighter. In general, however, form of spiral highly variable in individual animals, sometimes comparatively more open and sometimes very narrow.

Shaft of horn highly flattened, compressed from sides, and exhibits distinct anterior and posterior ridges. Anterior ridge blunt and posterior one sharper, especially in terminal portion of horn. Inner surface of horn flattened, sometimes even slightly concave, while outer surface convex.[221] Horns covered with small irregular annular
594 wrinkles, which are very sharp in terminal portion (very early segments). Margins of annual segments, as in other goats, distinct.

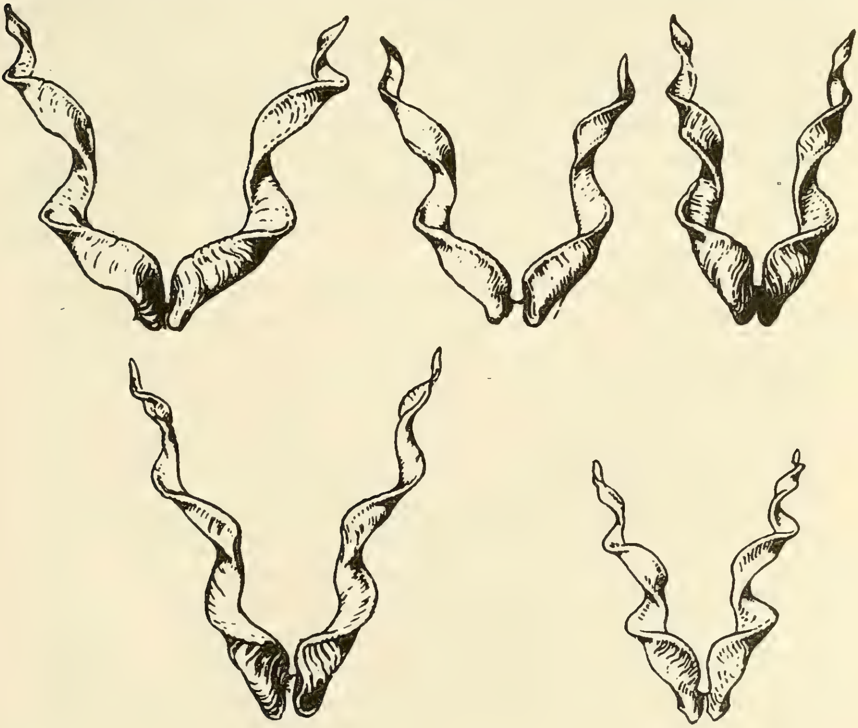
Horn bases invariably close-set, but angle at which they diverge highly variable in individual cases. Distance between horn tips may be 41 to 88% of horn length measured along curvature. Usually horns do not diverge intensely and are extremely close-set, running parallel in extremely rare cases. Lyrate, arcuate, or other types of bends of the horn axis absent. In the remaining features however, i.e., size, bulk, curvature, etc., the horns exhibit strong individual variations. Age-related changes also prominent. As a result of the characteristic horn structure, age-related variability is much greater than in other species. Horns of young animals are characterized not only by their general size but also by number and nature of twists.

Horns of females short and thin, twisted in the same manner as those of males, but weak and flattened from sides; rugosity less defined and margins of annual segments fainter.

---

[221] It should be remembered that the inner surface of the horn is exposed on the forehead in the first turn of a screw-shaped horn.

Pelage in winter dense and long with extremely abundant underfur; in summer it is short, sparser, and without underfur. In adult males large dense beard reaches 25 cm in length; beard in females smaller. Beard present even in very young animals; in males aged 14 to 15 months it is about 10 cm long. Adult males with long hair in the form of a mane on lower parts of neck and chest. In winter coat it is very luxuriant, dense, and long, and hair reaches 30 cm. Small mane of long, curly hair extends along upper part of neck and back. In winter this hair attains a length of up to 15 cm. Fully developed mane seen only in adult animals; it is almost undeveloped in yearlings, small in two-year-olds, and fully formed in four-year-olds.
595 In the summer coat sides, back, neck, and legs bright reddish-sandy color. Because of admixture of some gray hair, head appears darker. Abdomen and inner surfaces of legs whitish-gray, but lightest in region of groins. Tail black or with a black stripe. Beard long, dense, and wedge-shaped in profile. Front portion consists of pure



594 Fig. 208. Variation in horns of markhor, *Capra falconeri* Wagn., in the USSR. Original drawing by N.N. Kondakov based on material from the Zoological Museum of Moscow State University.

lustrous black hair and rear portion of dirty yellow or almost white hair. Mane of long whitish hair occurs on chest and neck. Between beard and mane on neck a section occurs in which hair is normal in length or only slightly elongated. Along midline of upper side of neck and back small light-colored mane occurs. Large bare calluses are found in carpal region, below which bright black bands run down the legs. Similar areas are also seen on hind legs.

Winter coloration of a general gray tone and somewhat resembles that of a wolf. In general, however, not much is known about it other than that it is highly variable. In young animals (one to three years) color lighter than in summer, rusty with an admixture of gray. Adult animals also known to be very light in color. Very long hair in this case almost white for much of its length and only tips a dark cinnamon. General tone of coat whitish with a bluish-brown shade. Head usually darker. At the same time a dark, brownish-gray coloration is also seen among adults (Heptner, 1940; Tsalkin, 1945).

Bony horn core fairly large and invariably twisted in the same manner as keratinous part of horn. In cross section core has a semicircular outline—a flattened inner surface and a highly convex outer one. Anterior and posterior ridges well developed; posterior ones sharper than anterior ones throughout length of core. Angle formed by bony cores, in general, variable to the same extent as indicated above for horns. Distance between bases of cores fairly variable in different individuals; in general, however, it decreases with age and with an increase in size of core.

Skull,[222] viewed from dorsal side, relatively quite elongated and narrow and orbits project markedly sideways (tubular). In front of the orbit and below it occurs a large depression, which sharply sets off the facial portion of the skull, giving it an elongated and narrow form.

Anteronasal profile somewhat concave in front of orbits, nasals long and greatly encroaching on frontals, and suture between them disappears completely fairly early. A perpendicular line drawn from anterior end of nasals to palatal surface will lie at a distance not greater than length of first two premolars from anterior end of tooth row. Premaxillae large, reach nasals, and usually wedged between them and maxillae. Surface of frontals bulges very slightly in transverse plane and almost straight in longitudinal one. Prominences absent on frontals in front of horns and their highest point (and of the skull itself) falls between the bases of the horns close to their

[222] See Figs. 177, 178 and 179.

posterior margin. Thus a sharp flexure of the frontals occurs in the sagittal plane.

Base of bony core of horn, compared with that in other species, greatly shifted toward posterior side. Posterior margin of base situated at a distance from orbit which exceeds diameter of latter, or at least is not less than this. Consequently skull behind horns extremely reduced; parietals are also greatly reduced. Parietals do not bulge; contrarily they are flat or even concave as in Dagestan tur (*C. cylindricornis*).

Skull of females differs in several features, all of which are essentially related to a far weaker horn development. Horn cores shorter, thinner, and wider-set; frontals do not bend sharply in sagittal plane; skull section behind horns descends more gently; forehead almost totally flat; distance between posterior margin of horn core and posterior margin of orbits less than diameter of orbits; parietals
596 are not concave but bulge. Some of these features are characteristic not only of females, but also of young males, and reflect a certain degree of infantilism.

Markhor are one of the largest representatives of the genus *Capra*. Body length of adult males 161 to 168 cm and of females about 140 to 150 cm; height at shoulders in males 86 to 89 cm, probably up to 100 cm; chest circumference of males 101 to 103 cm; tail length in males 12 to 14 cm and in females 8.0 cm; and length of ears in males 12 to 15 cm and in females 8.0 cm.

Length of horns in males six years or older (up to 10 years) found within the Soviet Union 58 to 73 cm measured in a straight line, and 75 to 90 cm along bends of spiral. Circumference of horn at base 21 to 26 cm; distance between horn tips 21 to 60 cm (41 to 88% of length along spiral).

The known maximum weight of adult males is 80 to 86 kg (May–June), which evidently can reach 100 kg, and of females is 41 kg, but probably could exceed 50 kg.

The maximum skull length in adult males varies from 260 to 290 mm and in females from 228 to 237 mm.[223] (V.H.)

Taxonomy

Markhor constitute a well-isolated species of the genus *Capra* and to some extent represent an extreme form of goat. This peripheral position among goats, more than anything else, provides a basis for separating this form into an independent genus, or at least a subgenus.

---

[223] The material available for this species in Soviet museums is extremely limited and data on measurements even more so. The world record of horn length along the spiral is 159 cm. Although Russian goats may not attain such dimensions, indubitably some Russian markhor do have larger horns than stated above. The description is based mainly on material from Flerov, 1935; Heptner, 1949; and Tsalkin, 1945. Measurements are mostly those given by Tsalkin (1945).

In the last decade more detailed studies of the various characteristics of goat, and not merely their horns as done before, have established that the degree of isolation of markhor from other species of genus *Capra* is less than previously supposed. Features of similarity to Dagestan tur (*C. cylindricornis*) have been detected—flatness and even concavity in the region of the parietals among others. Likewise the horn flexure of markhor can no longer be considered unique. It is somewhat reminiscent of that seen in horns of the Pyrenean goat (*C. pyrenaica*) and even more so horns of the Dagestan tur (*C. cylindricornis*). One should also remember that the characteristic skull features of markhor, given above, are largely associated with the structure of horns.

Yet while it is true that the features detailed above in some measure bring markhor close to other species of genus *Capra* and diminish its differentiation, still several highly distinctive features must be acknowledged. The mane and tress on the neck and chest differ from those of other species. Even in structure of horns there are distinctive features, particularly their flatness. The horn of markhor, figuratively speaking, is more the twisted type seen in bearded goat (*C. aegagrus*) than in Dagestan tur (*C. cylindricornis*) or Pyrenean goat (*C. pyrenaica*).

All this compels one to recognize markhor not only as a well-isolated species, but also to elevate it to the rank of subgenus. Attempts to merge it with remaining goats as a subspecies under the broadly interpreted species, *C. ibex,* often suggested in the recent past, cannot be justified. This extreme tendency to combine species "at any cost" has as little relevance to modern concepts of species as the extreme splitting of species, and is highly detrimental to taxonomy.

The geographic relations of this species with other goats also point to its independence (see "Geographic Distribution" below and sections on Siberian ibex *C. sibirica* and bearded goat *C. aegagrus*). (V.H.)

597

Geographic Distribution

Markhor are found in the mountains of northern and northwestern India, Baluchistan, and Afghanistan, and the mountains on the right bank of the lower Pyandzha and upper Amu-Darya.

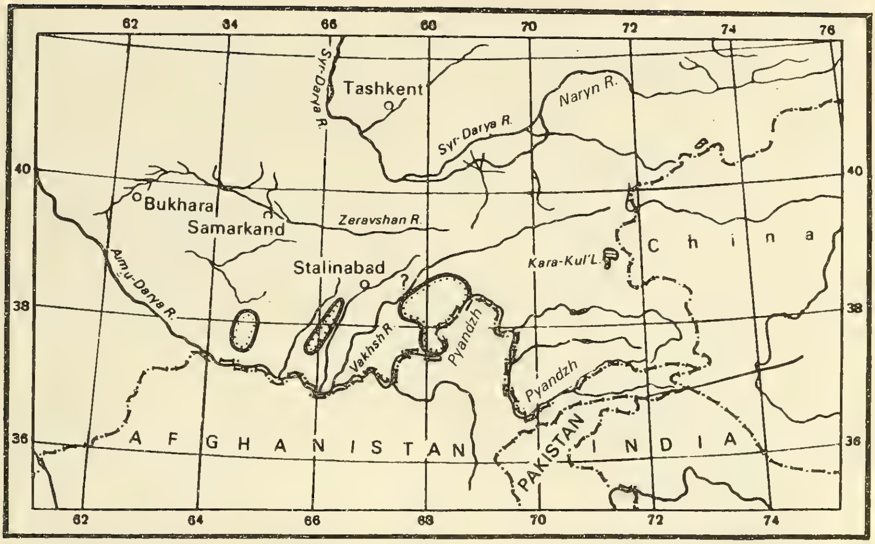

Tashkent
Syr-Darya R.
Naryn R.
Bukhara
Samarkand
Zeravshan R.
Stalinabad
Kara-Kul'L.
China
Amu-Darya R.
Vakhsh R.
Pyandzh
AFGHANISTAN
PAKISTAN
INDIA
?
62
64
66
68
70
72
74
76
40
38
36

Fig. 209. Range of markhor, *Capra falconeri* Wagn., in the Soviet Union. Range not totally restored but somewhat more extensive than at present. V.G. Heptner.

Geographic Range in the Soviet Union

The range in the Soviet Union represents the extreme northern edge of the species' range and occupies an insignificant part of the territory of the Soviet Union, in the region of upper Amu-Darya. The range here is not continuous but broken into several sections.

One section of distribution of markhor covers the Kugitangtau massif close to the Amu-Darya, which are a continuation of the Baisunsk mountains to the south. In the eastern (Uzbekistan) part of Kugitangtau markhor are found around Vanda *kishlak* [village] and Atly-Kunik, Bidak, Uzil'ma, Aral, Tangi-Duval, Kattatag, Chungul'-Darya, Zarvus, and several other gorges. A significant number of goats are known to inhabit the western (Turkmenian) side of the range. The northern limit of the range is evidently represented by the region of Tangi-Duval gorge commencing at Khatak village and extending for some dozens of kilometers westward. This gorge divides Kugitangtau from the Gissar mountain (Sultanov, 1953).

In the Baisunsk mountains, in spite of some circumstantial evidence, markhor are absent.[224]

[224] Horns of this species have purportedly been found in tombs in Shirabad and Baisun (Trubetskoi, 1910). If these reports are accurate, not only the horns found in

A second region of distribution of markhor, wholly isolated from the others, covers the Babadag range located between the middle courses of the Surkhan-Darya and Kafirnigan. Details about the distribution of this goat here are not known (Sultanov, 1953).

The third habitat of markhor within the USSR lies eastward. Information about it is not very precise. It covers the mountain regions adjoining the Pyandzha from Darvaza in the east and northeast[225] down along the Pyandzha to a line from Kulyab to 598 Chubek. It also extends to the mountains on the divide between the Pyandzha and Yakhsu (left tributary of the Kyzyl Su on which Kulyab stands); markhor occur there in the Hazrat-Imam-Askariya massif (roughly 20 km east of Kulyab; about 3,000 m), and in the southern extremity of the range extending toward the Pyandzha (Kishvaristan mountains) and on the slopes of the Pyandzhas (Trubetskoi, 1910). They also occur in the region of Dashtidshum, northeast of Kulyab, located in the same montane watershed system. Data are not available on the boundary of distribution of markhor in the east and north.

The region of Bal'dzhuan and evidently also the Vakhsh range forms part of the geographic range. References to Karategin ("Karateginsk bekstvo"—Karateginsk mountain range? V.H.) are not definite but this region should possibly be included in the range of markhor.[226]

No positive data are available for the expanse between Kugitangtau and Babadag and for the just described eastern areas of occurrence of markhor; it does not live there and was not apparently present there in the period under review. Yet based on zoogeographic and ecological considerations there is adequate justification to consider that the range of markhor in the past was greater than what has been described. They were probably present throughout the expanse between Darvaza and Karategin on one side and Kugitang-

the first place, located very close to Kugitangtau, but also those found in the second place, located at a much greater distance from Kugitangtau, must have been collected from animals living in the Kugitangtau massif per se.

Highly contradictory information is available about markhor in the Baisunsk mountains in the region of the Sangardak River and at some other adjoining points (Baisunsk, Yakkabag, Dakhkanabad, Guzar, Denausk, and Sary-Assiisk regions of Uzbekistan) (V.G. Heptner; Sultanov, 1953).

[225] Evidently the region within the arc of the western part of the Darvaza range—slightly to, or almost directly east of Kalai-Khumb.

[226] For this region, at present, based on labeled specimens, the following localities of occurrence of the animal have been shown: Sarkharya mountains in Bal'dzhuan, Tabakcha mountains in "Eastern Bukhara," Sanktuda at the same place, Terkla mountains in Kulyab (mainly data of Flerov, 1935), and the Dashtidshum region.

tau on the other. However, the distribution could not have been continuous since the valleys of the Pyandzha tributaries are broad and extensive. Interfluve mountains, though not very high (mountains of the watersheds of the Vakhsh and Kafirnigan, about 2,200 m) are wholly favorable for the survival of this species, members of which lived even at low altitudes.

The range outlined above, insofar as Kugitangtau and Babadag are concerned, has been compiled on the basis of data for the end of the last century (from the 1880's) and mainly for the early years of the present century. Data are not available about the extent of the range at the present time. In Kugitangtau and Babadag this goat still survives in sufficiently large numbers. It is absent in the Karateginsk range but is still encountered on the spurs of the Vakhsh range (Sanglok mountains) and includes the region described on the divide between the Pyandzha and Yakhsu, in particular the Dashtidshum region.[227]

Geographic Range outside the Soviet Union

Outside the Soviet Union the range covers Afghanistan, but no details of the distribution of goats in this region are available. It is only known that they live in northern Afghanistan and in the Hazarajat country (central and southeastern parts of Afghanistan). It may be assumed that at the highest altitudes of the Hindu Kush and along the main axis of this range markhor probably are not present, and its range is confined to the lower and middle altitudes of this system. It is highly probable that its sporadic distribution is due to extinction.

Markhor occupy the Quetta district in Baluchistan, but evidently do not occur any farther southwest and south from there.[228] Somewhat farther east the range extends to all of the Sulaiman mountains without extending into the left lowland bank of the Indus. In the Sulaiman mountains these goats are known in the region southeast of Quetta, Dera Ghazi Khan (30° N lat.) and Dera Ismail Khan. Farther north the range enters the Peshawar district, the Swat district to the north, and Chitral. From there to the east the range encompasses Gilgit, Astor, and Baltistan (region of the northern branch of Indus), the Kashmiri part of the Himalayas (evidently, not east of the Sutlej), the Pir-Panjal range enclosing the Kashmir valley

---

[227] The range is based on data from Trubetskoi, 1910; Flerov, 1935; Heptner, 1940; Tsalkin, 1945; and some original unpublished material of V.G. Heptner and V.I. Chernyshev.

[228] See the section on bearded goat (*C. aegagrus*).

599 on the south, and the small elevation Kai-nag in Kashmir west of the Jhelum River. In the south the range does not reach the Solan hills and this species is absent in the Punjab along the left bank of Indus.[229]

Within the USSR the markhor is allopatric with the Siberian ibex (*C. sibirica*) and their ranges in the Amu-Darya basin, where they come closest, evidently do not adjoin each other and probably never did so in the past. However, in Afghanistan and in some parts of northeastern India (Kashmir, Baltistan, Gilgit, etc.), the two species over much of the area occupy the same geographic territory. Details of their biotopic and biological relations are not known, but some extremely vague information suggests that the two species occupy different levels of the mountains—Siberian ibex occupying higher levels and markhor much lower levels.

Such a separation, even if it does exist, cannot be total and the animals undoubtedly encounter one another. If markhor do not ascend to extreme heights, Siberian ibex are capable of living over a wide range of altitudes. Thus, at several places in northern Afghanistan, very warm and dry (Afghan Badkhiz) Siberian ibex live at very low absolute and relative altitudes (Thomas, 1889; Heptner, 1956). Nevertheless information is not available in the literature about hybrid populations or hybrid individuals of these species. The relationship between these species at some places is probably similar to the relationship between bearded goat (*C. aegagrus*) and Dagestan tur (*C. cylindricornis*) in the Caucasus (Heptner and Formozov, 1941). There is a reference that markhor lived in the forest zone at some places in India (Prater, 1947).

The congruence of a significant part of the range of markhor with that of other species of the genus serves as proof of its independence as a species (see the section on taxonomy and sections on Siberian ibex *C. sibirica* and bearded goat *C. aegagrus*). (V.H.)

Geographic Variation

Over a comparatively small territory of the range of the species, seven (one has not been formally named) geographic forms have been identified. All are characterized by the structural features of their horns. As mentioned before, this feature is highly variable and the actual number of subspecies is obviously less. It is significant

---

[229] The range outside the Soviet Union is mainly based on data from Lydekker, 1913; Prater, 1947; and other sources.

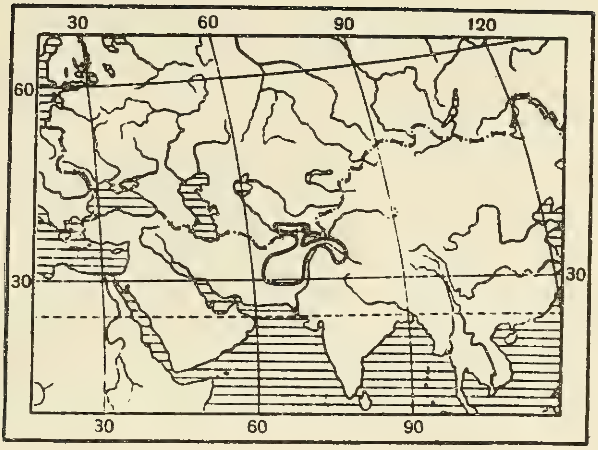


Fig 210. Species range, partly reconstructed, of markhor, *Capra falconeri* Wagn. V.G. Heptner.

that the type localities[230] of some forms (*megaceros, jerdoni,* and *chialtanensis*) fall in close proximity at Kandahar in Afghanistan, Quetta in Baluchistan, and the Sulaiman mountains. This by itself gives rise to doubts about the independence of these subspecies. The 600 forms *falconeri* and *kashmeriensis* have been described from Kashmir (Astor and Pir-Panjal mountains) and a third has also been noted from there (Gilgit).[231] The type localities of the two described from the USSR (*heptneri* and *ognevi*) also fall quite close to each other (see below).

Taking into consideration the topography of the region of habitation of the species, its geographic variation can hardly be disputed as is sometimes done (Flerov, 1935). Yet there is apparently no basis for recognizing all the six described forms. Geographic variation of the species requires complete revision.

Only one form is found in the Soviet Union.

Bukhara screw-horned goat or markhor, *C. f. heptneri* Zalkin, 1945 (syn. *ognevi*).

This subspecies is described above; it is probable that this form is also characterized by small-sized horns.

Found in the mountains on the right banks of the lower

---

[230] Information based on Ellerman and Morrison-Scott (1951). Information provided by Lydekker (1913) is usually less accurate and differs from the former.

[231] Astor is a town and a river (left tributary of the upper Indus) lying east of Nanga Parbat peak (8,126 m), southwest [southeast—? Translator] of the town of Gilgit. The Pir-Panjal range extends along the Himalayas from Indus to the southeast. The boundary of its northwestern quarter lies south of the city of Srinagar.

Pyandzha and upper Amu-Darya from the Kulyab district to Kugitangtau inclusive. It has not been recorded outside the USSR; possibly, it is found in northern Afghanistan.

The taxonomic differences in goats within the USSR have not been thoroughly studied. Evidently, however, this form is justifiable. This is the northernmost form of the species inhabiting a territory which is well isolated from the rest of the range. There are no apparent differences between the goats of the Kulyab district and those of Kugitangtau, from whence the form *ognevi* has been described. Moreover, these two populations, though now well isolated, no doubt were contiguous in the relatively recent past.

Outside the Soviet Union the following forms are usually recognized: *C. f. falconeri* Wagn., 1839—Baltistan, Indus valley; *C. f. megaceros* Hutt., 1842—Kandahar district and southward to Baluchistan; *C. f. jerdoni* Hume, 1875—Sulaiman mountains; *C. f. cashmeriensis* Lyd., 1898—Pri-Panjal range; and *C. f chialtanensis* Lyd., 1913—mountains by Quetta in Baluchistan. The last form is probably based on a hybrid of markhor and bearded goat (*C. aegagrus*). (V.H.)

Biology

Population. In the Soviet Union the numbers of markhor are not large, less than 1,000. Half a century ago in the Kugitangtau mountains (Uzbek and Turkmenian Soviet Socialist Republics) these goats were even fewer than now (Sultanov, 1953); evidently greater numbers lived around Kulyab.

Habitat. In the Kugitangtau the majority of markhor live at altitudes of between 1,500 to 2,500 m, but they avoid dense clumps of juniper and are most often sighted along the slopes of deep gorges where there are many rocks and even meadows covered with herbaceous steppe vegetation and sparse shrubs. Some of the animals, especially adult males, are found in summer up to the highest summits of the range (3,000 to 3,500 m) covered by montane steppe ("alpine") meadows (Sultanov, 1953). In the Kulyab district male markhor in summer ascend even higher, sometimes entering the upper alpine meadows ("mats") adjoining the permanent snow line. Females and young are not encountered that high (Trubetskoi, 1910). Nevertheless, compared with Siberian ibex, markhor tend to be seen in the less elevated parts of mountains. This is true not only of the Soviet Union but of other parts of their range, not excluding the Himalayas.

Food. The food regime has been little studied. The main food of

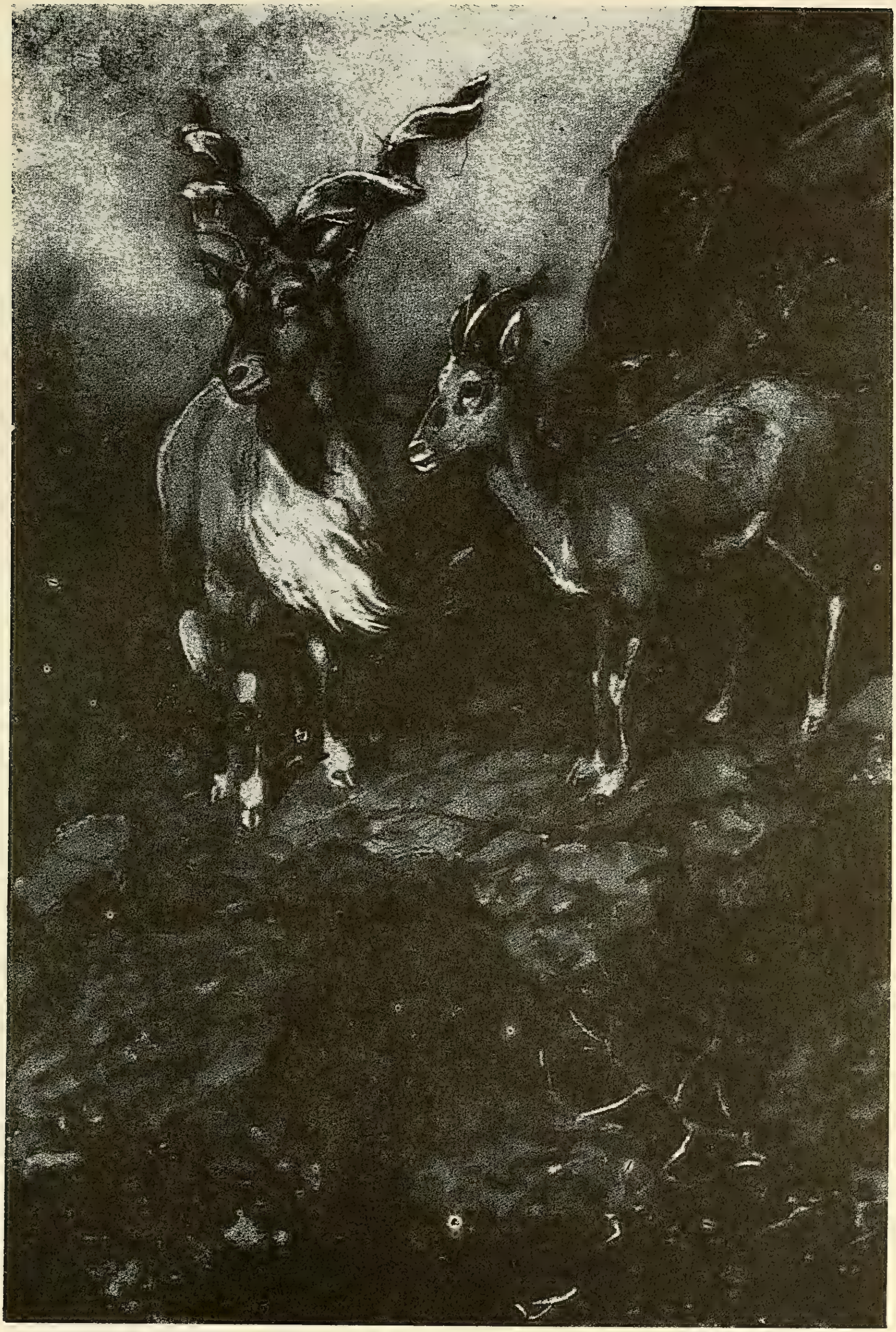


Plate 5. Markhor, *Capra (Orthaegoceros) falconeri* Wagn.
Painting by A.N. Komarov.

markhor is herbaceous vegetation and, to a lesser extent, leaves, twigs, shoots, and also bark of shrubs and some trees.

In the Kugitangtau these goats consume year-round some grasses
601 (meadow grass, brome grass, and others), sedges, origanum-like ziziphor, Turkestan maple, Bukhara almond, cotoneaster, red cherries, honeysuckle, and others. In spring the young shoots, and in winter the dry leaves, of Maximovich rhubarb are consumed. Sagebrush and the tender needles of Zeravshan juniper are consumed predominantly in winter and that, too, in large quantities (goats eat only the thin tender branches of old trees); Umbelliferae, *Prangos pabularia*, and *Ferula jaeshkeana* are of some importance in the winter food of goats. Goats usually do not dig up food from under the snow and are satisfied with that freely accessible above it, in addition to browse. In summer they visit water holes; snow replaces water in winter (Sultanov, 1953).

Home range. Dimensions have not been established.

Daily activity and behavior. In the Kugitangtau markhor in summer graze at night, dusk, and early morning hours. By 10:00 a.m., having visited the water hole, they rest in their beds in shaded spots among rocks, sometimes concealing themselves under the protection of shrubs. At sundown they visit the water hole again, after which they begin to graze. Water holes in the Kugitangtau are rare and are often located a kilometer away from goat beds. In winter goats graze throughout most of the day and at night move into cliff areas seeking protection from the wind (Sultanov, 1953). Markhor can easily negotiate even very steep slopes; their hooves are characterized by great mobility and can spread apart widely. In the event of danger the animals seek protection on cliffs. They are not capable of prolonged fast running.

Adult males and females live for much of the year separately, forming groups of three to five, rarely more. Immature males and juveniles move with females. The herding instinct is strong in winter; groups of up to 27 animals have been observed in the period of rut (Sultanov, 1953; and others).

Seasonal migrations and transgressions. Seasonal migrations are characteristic of markhor. In the Kugitangtau the range of vertical seasonal migrations usually does not exceed several hundred meters and most goats are confined in winter to only slightly lower levels than in summer, remaining within the same belt of sparse juniper woodland (from 1,500 m and above) in which they live in June and July. Many goats remain in summer habitats well into autumn. Only in extremely snowy and severe winters do some descend into wheat grass–mixed grass steppes, rarely moving even into ephemeral semideserts and to ranges located at heights of less than 800 m above sea level (Sultanov, 1953). Areas covered during seasonal migrations of markhor in the Kulyab district are significantly broader, while in winter goats are confined to many hundreds of meters lower than in summer. Migrations occur early; even in September females are sighted in the mountain belt below the upper limit of grainfields to which level Siberian ibex usually do not descend. Markhor remain there until early spring (Trubetskoi, 1910).

Reproduction. In the Kugitangtau rut in markhor occurs from the first half of November to around December 20 and is accompanied by serious combats between adult males. At this time of year goats are encountered in groups of significantly mixed composition; young and weak males move away from the herd. Males in rut are highly weakened by the end of it (Sultanov, 1953). In Moscow Zoological Garden rut in markhor occurs from the end of November through early January (Tsalkin, 1948).

Gestation in goats lasts about six months. Before parturition the female separates herself from the herd. Mass births in the Kugitangtau occur from the end of April to early May. In a zoological garden births were recorded from the end of April to the first few days of June, the majority occurring in May. The female produces one or two kids (Trubetskoi, 1910; Tsalkin, 1948; Sultanov, 1953).

Sexual maturity apparently is not manifested during the third year as usually reported, but in the second as in other species of genus *Capra*. In fact most females probably take part in breeding only in their third year, while males do so at a much later age.

Growth, development, and molt. Kids freely follow their mothers even on the second day after birth. Lactation continues right into
602 autumn, sometimes for five or six months. These goats live for ten years or more. The weight of adult males exceeds 80 kg.

Periods of molt have not been established. Molting markhor have been observed in the second half of April and in May. Molt commences from the lower part of the trunk, with the back molting later (Sultanov, 1953).

Enemies, diseases, parasites, mortality, competitors, and population dynamics. Wolves inflict some damage on markhor. These predators may be dangerous in cases when goats are far away from cliffs, on gentle slopes. References that lammergeier threaten juveniles are not supported by direct evidence. There are no other references in Soviet literature to the enemies of markhor.

Markhor suffer from gadflies, blood-sucking insects, and various helminths. In zoological gardens instances have been recorded of death due to necrobacillosis.

The main competitors of markhor in Kugitangtau pastures are herds of domestic animals.

Field characteristics. Markhor differ from Siberian ibex in screw-shaped horns (horns of the latter are arcuate) and the presence of a mane in adult males in the lower part of the neck and chest. Horns of females are perceptibly smaller than those of males. The presence of these goats in a region can be established by the presence of their feces, hoofprints, and trails in areas of their routine movements. (A.N.)

Economic Importance

Markhor yield excellent meat (weight of carcass 80 kg or more), tough hides, and beautiful horns, used mainly as wall decorations. The meat is best in autumn up to the commencement of rut. Markhor live well in captivity, including zoological gardens, where they multiply and also interbreed with other species of goats.

These goats are shot with rifles by ambushing them on trails, stalking, or by driving them. The maximum number of animals are caught early in spring (when the quality of meat is poorest since goats are often malnourished at that time of year). According to Sultanov (1953) 151 hides of markhor were received by the Shirabad processing unit in Uzbekistan from January 1 through May 25, 1935. Hunting these animals was banned in 1936 in view of their small numbers. (A.N.)

Genus of Mountain, or Rock, Sheep

Genus *Ovis* Linnaeus, 1753

1758. *Ovis*. Linnaeus. *Systema Naturae,* 10th ed., p. 7. *Ovis aries* Linnaeus (domestic sheep).

1762. *Aries*. Brisson. *Regn. Anim.,* p. 12. *Aries* Brisson = *Ovis aries* Linn.

1776. *Musimon*. Pallas. *Spicil. Zool.,* vol. 11, p. 8. *Musimon asiaticum* Pall. = *Capra ammon* Linn.

1798. *Musmon*. Schrenk. *Fauna Boica,* vol. 1, p. 81. Substitute for *Ovis* Linn.

1816. *Ammon*. Blainville. *Bull. Soc. Philom. Paris,* p. 76. Substitute for *Ovis* Linn.

1847. *Caprovis*. Hodgson. *Journ. Asiat. Soc. Bengal,* vol. 16, p. 702. *Ovis musimon* Pall.

1852. *Argali*. Gray. *Cat. Mamm. Brit. Mus.,* vol. 3, p. 74. *Aegoceros argali* Pall. = *Ovis ammon* Linn.

1936. *Pachyceros.* V. Gromova. *Neue Forschungen in Tierz. und Abstammungslehre* (Festschr. Dr. Dürst), p. 84. *Ovis nivicola* Esch. (V.H.)

Species of moderate, but sometimes less than moderate, or even large, size. Build stout but not heavy and legs long and thin.

Metacarpals (compared to *Capra*) relatively long and thin (maximum diameter of diaphysis not more than 10% of length of bone).

603 Facial part of skull normally developed. Skull behind horns reduced and set relatively steeply. Flexure of anteroparietal region of skull large. Skull highly pneumatized. Ethmoid pit absent or faint. Nasals normal in structure (not shortened) and join frontals, lacrimals, and maxillae. Ascending processes of premaxillae fairly long and wedged between nasals and maxillae, or short, not reaching nasals. Nostrils not enlarged and lacrimals of normal structure (not reaching nostrils). Depression ("tear pit") on lacrimals usually large, with a longitudinal crest. Infraorbital foramen small. Basal portion of bony core of horn not elongated (on skull, distance from edge of horn sheath to upper edge of orbit smaller than maximum diameter of orbit). Profile of skull behind horns slightly convex or nearly straight. Coronal [fronto-parietal] suture forms an angle, is set forward, and the lambdoid [parieto-occipital] suture forms a straight line or is arcuate. Crests on parietals wide-set (smallest distance between them more than length of parietals along midline).

Dental formula:

$$\mathrm{i}\frac{0}{3},\ \mathrm{c}\frac{0}{1},\ \mathrm{pm}\frac{3}{3},\ \mathrm{m}\frac{3}{3} = 32.$$

Posterior and median vertical ridges present on outer surface of upper premolars.

Male horns extremely diverse in size, curvature, and form in cross section. Usually they are large and massive and broad at base (difference between circumference of horns at base and in last one-quarter considerable).

Horns can be classified under three main types according to the nature of their curvature. The heteronymous [supracervical] horn at its base is turned up, back, and out, while the terminal portion is turned in toward the neck and fairly horizontal. Horn tips situated above the neck and face each other. Sometimes tips set inward and slightly up. Thus when the skull and horns are viewed from the rear, terminal portion of right horn appears bent to the left, and left horn turned to the right (the reverse seen when the skull is viewed from the front: right, to the right; left, to the left). This is negative curvature of horns.

The homonymous horn initially turns up, back, and out, and later down, forward, and out. Thus the horn ends do not face each other but opposite directions or are quite parallel. In horns of this type the spiral of the right is twisted to the right and its end turned right, while the left horn is twisted to the left (reverse pattern when skull viewed from the front). This is positive curvature of horns.[232]

The third type, known as perverted [cervical] horn, has something of an intermediate structure between the above two main types. Initially they are directed up, back, and out, and later, in the terminal half, curve down and in toward the neck. In an extremely typical case the horn is thus bent in a single plane. The degree of horn perversion may vary, however. The terminal portion may deflect insignificantly in a positive (outward, away from the neck) or in a negative (inward, toward the neck) bend.[233,*]

In most cases horns are homonymous, less often perverted, and rarely heteronymous. Horns set fairly vertically and bent back like a scimitar in a single plane, as in some goats, do not occur. Knobs and sharply projecting large transverse ribs are absent on the anterior horn surface.

604 Cross section of horn at its base usually triangular with sharp or somewhat rounded outline and usually with a distinct, flat, frontal surface. Horns with oval, lenticular, or drop-shaped cross sections not found. Keratin white (with the exception of one form—mouflon *O. ammon musimon* in which dark).

Horns of females small, fairly straight, and bent back insignificantly. In a few forms altogether absent, or females with and without horns seen.

Muzzle normal (not elongated or projecting in the form of a proboscis) and nostrils set forward. Bare area at end of muzzle very small and covers space between inner corners of nostrils and narrow strip along inner half of upper edge of nostrils; bare depression also extends from upper edge of lip to space between nostrils. Preorbital and inguinal glands present, carpal glands absent, and hoof glands present on all four limbs. Odoriferous caudal glands absent. Tail covered with hair on ventral surface but together with hair less than length of ear. Caudal vertebrae seven.

---

[232] The degree of positive or negative curvature is highly variable. Other examples of positive types of curvature are: horn tips only slightly bent outward and set forward (when the horns are relatively small), or the horns form a second spiral and their ends are turned straight sideways and lie horizontally at a right angle to the sagittal plane of the body.

[233] The above terminology was introduced into Soviet literature at the beginning of the century by N.V. Nasonov and gained acceptance. It is not particularly helpful, primarily because complex, and often wrongly used. Moreover, the meaning of some terms in the Soviet Union differs from what they convey in western Europe (see the description of argali sheep given later).

*Valdez, "The Wild Sheep of the World", Mesilla, NM, 1982, used *perverted* for supracervical or heteronymous, in contrast to the present volume—Sci. Ed.

Pelage of equal length, but relatively short (not shaggy). Beard on chin, seen in goats, absent in these animals, but large tress below neck and partly on chest occurs in winter coat of some forms. Color usually uniform light shades of yellow, more rarely cinnamon, much lighter below; sometimes light-colored area occurs on flank and white coloration along neck and chest. Seasonal dimorphism in density and color of coat generally pronounced, and variation in formation of tress is observed. Sexual dimorphism quite pronounced. Females smaller, with small simple horns, or without horns and without tress. Teats two (sometimes two additional rudimentary teats also present).

Overall appearance quite characteristic and very different from that of domestic sheep.

These are montane animals confined mainly to regions with relatively smooth terrain. They exhibit no distinct attraction to rocky areas, or are associated with them to a limited degree only in some places. They are encountered from sea level to heights of over 5,000 m but associated more with low and middle altitudes. They usually live in small herds but form larger ones under certain circumstances.

The range of the genus occupies several islands in the Mediterranean Sea, the Near and Middle East, Central, northeastern and partly northern Asia, and western North America. Sheep are encountered (reconstructed range) in Corsica, Sardinia, Cyprus, mountains of the southern half of Asia Minor,[234] mountains of Turkish Armenia (including the Erzurum region), south of the central Trans-Caucasus, Iran south to Luristan, Afghanistan, Baluchistan (Sulaiman mountains), northern Punjab, Kashmir, Ladakh, eastern Himalayas to the region north of Sikkim (wandering into Kumaon and Nepal), in the Kunlun, Altyntagh and its western continuation (Kerii and Russkii ranges), Nan Shan and northeastern Tibet (including the region at the sources of Yellow River), mountains of Inner Mongolia (Ala Shan, Yabarai, and others), northern Shansi, southern part of the Great Khingans, the Mongolian Republic, eastern part of the Tien Shans, Kashgaria and Dzhungaria. The range also covers Middle Asia in the north to the northern Chink of the Ustyurt and Mangyshlak, Sultan-Uizdag, Karatau, Ulutau and Ortau (near Akmolinsk), Saur, Altai, Sailyugem, Tannu-Ola, Khamar-Daban, and Stanovoi ranges, montane regions of northern Siberia from Anadyr territory almost to the mouth of the Yenisey (Syverma and Noril'sk mountains), at places to the shore of the Arctic Ocean and Bering Sea, Kamchatka, and probably the northern Kuril Islands (eighteenth century). In North America the range covers Alaska, 606 including the Kenai Peninsula (in the remote past probably the Aleutian range), east almost up to the Mackenzie, and along the western half of the mainland south to Mexico (Baja California and Chihuahua), and east to Texas, Nebraska, and the Dakotas (roughly 100°).

---

[234] More precisely, Kilikii Taurus [Daglari] (Bulgardag [Bolkar Daglari] and Aladag [Ala Daglari] and Antitaurus, in the northwest including the Sultan, in the north to Konya and Aksaray, southeast of Lake Tuz-Kul' (Tuz-Chollu). Sheep are absent and were apparently absent at least in the last century in the Ankara region and all of the expanse north of these places up to the Black Sea, i.e., in Pontic mountains also.

Following the contour of the mountain ranges, the geographic range is broken up into a significant number of individual sections which at places are completely isolated. Sheep are now extinct in some regions and isolation thus intensified. In the past, due to favorable habitats in the plains and ease of migration from them, isolation was much weaker.

Sheep are acclimatized at several places on the European mainland (Crimea, Rumania, Poland, Hungary, Czechoslovakia, Yugoslavia, Italy, Germany, Holland, Switzerland, and Luxembourg).

Genus *Ovis* represents the most specialized group of the tribe Caprini, highly evolved and one of the extremely specialized groups of Bovidae on the whole. Genus *Ammotragus* (Barbary wild sheep, one species) is closest to genus *Ovis*. Sometimes the former is regarded only as a subgenus of *Ovis*. Goats of genus *Capra* are undoubtedly very close to genus *Ovis*, a fact repeatedly emphasized from very ancient times. The separation of these two groups is difficult in some respects, all the more so since genus *Ammotragus*, like genus *Pseudois* (Central Asiatic nahur [blue sheep] or kukuyaman, one species), occupies essentially an intermediate position between *Capra* and *Ovis* in several characteristics. The merger of all these forms into a single genus would appear natural from certain viewpoints but would require substantial evidence.[235]

The earliest fossil forms of genus *Ovis* are known from the Upper Pliocene of Asia (*O. zdanskyi* and *O. shantungensis*—China) and Europe. In North America these sheep are known only from the Middle Pleistocene, i.e., the group should be considered Asiatic or Eurasian in origin. The earliest representatives of this group,

---

[235] Additional data are given under the characteristics of genus *Capra*.

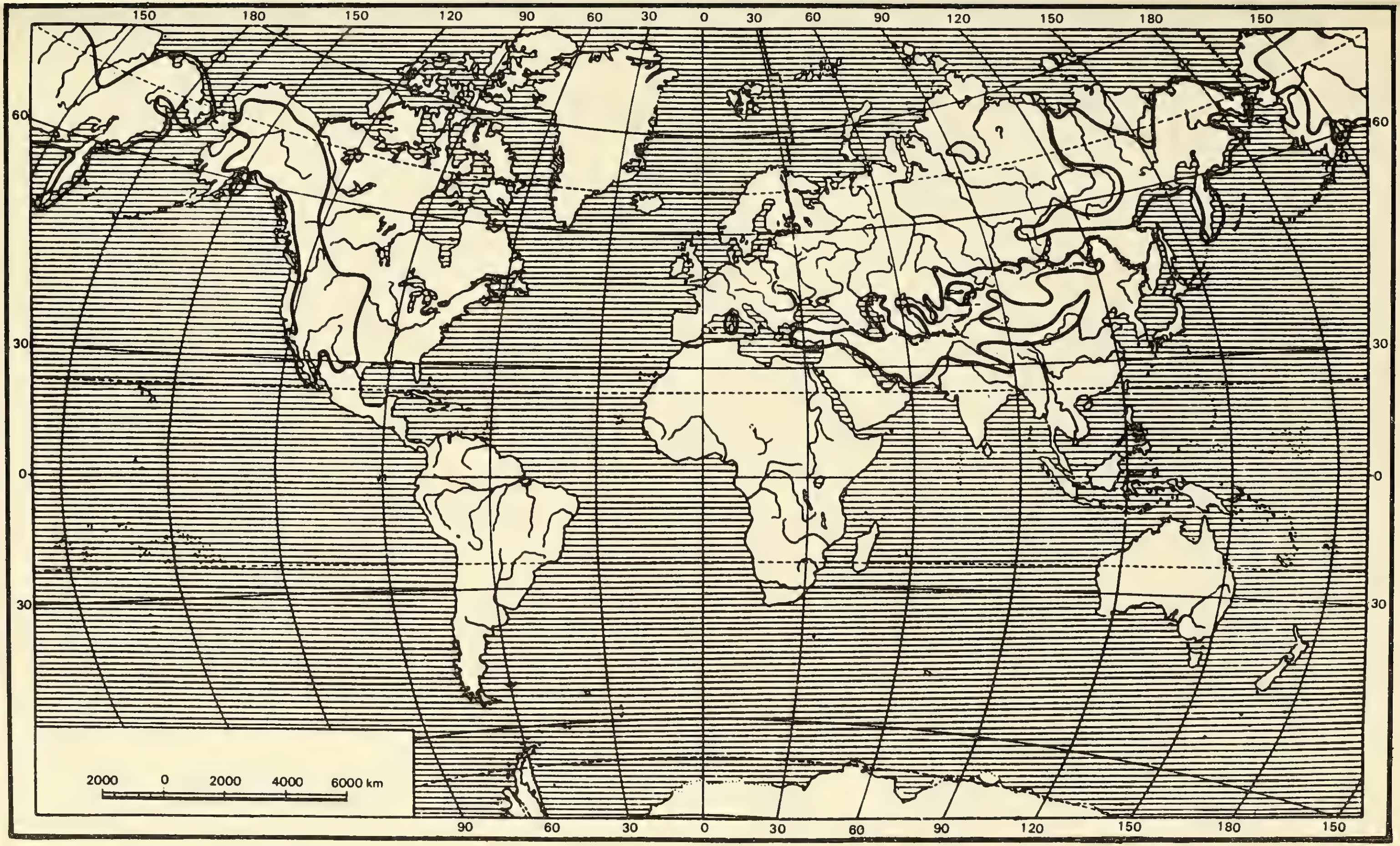

150
180
150
120
90
60
30
0
30
60
90
120
150
180
150
60
30
0
30
2000
0
2000
4000
6000 km

Fig. 211. Reconstructed range of genus of mountain sheep, *Ovis* L. (scale in km). Range in North America and north of the northern extremity of Baikal represents reconstructed range of species of bighorn sheep, *Ovis canadensis* Shaw; the rest represents reconstructed range of species of argali sheep, *Ovis ammon* L. V.G. Heptner.

belonging to genera now extinct but known from the Lower Pliocene, were also Asiatic forms. Two Pleistocene genera of the tribe are known from Africa.

In the Pleistocene argali sheep were distributed somewhat more extensively than at present, and in some places were quite numerous. They are known from Krasnoyarsk, around Irkutsk, the Tom' basin, Azerbaidzhan, Crimea, around Sochi, Chernigov district, Moravia, Hungary, Austria, Bulgaria, Germany, Italy, France, and even England. These sheep probably existed in the Crimea and Carpathians even in the Bronze Age (V. Gromov, 1948; Pidoplichko, 1951). In Europe, where the range of argali sheep is now limited only to some islands in the Mediterranean Sea, these animals in the past were quite widely dispersed and, in some cases, their distribution did not adhere so closely to montane regions.

Quaternary sheep were closely related to recent forms and evidently represented forms of recent species.[236] Among them are present-day forms resembling Kamchatka sheep (*"O. nivicola tomensis"*) and forms resembling the *ammon* group and mouflon group (*"O. argaloides"*).

Genus *Ovis*, as defined here, is fairly monolithic and past as well as recent attempts to divide it into two genera, or recognize subgenera within it, are not justified. The *O. ammon* group, considered here a species, has been divided into two genera (Severtsov, 1873). The western mouflon-like forms, commencing from Mangyshlak and Iran, have been designated as *Musimon*, and the eastern forms as *Ovis*. The very large and sharp geographic variation of the species did not fit into concepts of species in the 1860's and thus served as a basis for such a division. In another case (Gromova, 1936) two of the species under consideration here were placed in different genera—*Ovis* and *Pachyceros*.

607 Various authors (excluding older ones) have recognized, and do so even now, a different number of species in the genus: nine (Nasonov, 1923), five (Ellerman and Morrison-Scott, 1951), three (Flerov, 1932), and two (Tsalkin, 1951) in Eurasia. Here, the genus is considered to comprise two species (9.0% of the species of the subfamily): the Eurasian argali sheep, *O. ammon*, and the Asiatic-American snow sheep or chubuk, *O. canadensis*.[237]

---

[236] The independence of species of some Quaternary sheep (*O. sawignii* and *O. argaloides*) was based on the widely prevalent view that present-day sheep of the group *ammon* constitute not one but several species. Within the framework of geographic variation of this species, as interpreted here, differences in fossil forms do not appear so significant.

[237] Some acknowledge the existence of two species in North America: *O. dalli* and

Domestic sheep ("*Ovis aries*"), important farm animals, belong to genus *Ovis* and apparently originated from Mediterranean and Near Eastern forms.

Both species of the genus—*O. ammon* Linnaeus, 1758 and *O. canadensis* Shaw, 1804—are present in the Soviet Union.They constitute 0.6% of the total number of species of the Russian fauna.

These animals inhabit montane regions of the Trans-Caucasus, Middle Asia, and Kazakhstan, and southern, eastern, northern, and northeastern Siberia.

They are montane forms confined to regions with predominantly gentle sloping terrains and are encountered from sea level to very high altitudes.

These sheep are game animals but killing them is often prohibited. (V.H.)

21. MOUNTAIN SHEEP, ARKHAR[238]

Ovis ammon Linnaeus, 1758

1758. *Ovis ammon.* Linnaeus. *Syst. Naturae,* 10th ed., vol. 1, p. 70. Bukhtarma, Altai.[239]

1774. *Ovis orientalis.* Gmelin. *Reise d. Russl.,* vol. 3, p. 432. Eastern part of Elburz, Iran.

1776. *Musimon asiaticus.* Pallas. *Spicil. Zool.,* vol. 11, p. 8. Upper course of Irtysh.

1785. *Ovis argali.* Boddaert. *Elench. Animal,* p. 147. 1811. *Aegoceros* 608 *musimon.* Pallas. *Zoogr. Rosso-Asiat.,* vol. 1, p. 230. Eastern coast of Caspian Sea.[240]

O. canadensis. However, *O. dalli* simply comprises geographic forms of *O. canadensis* from the extreme northwestern mainland (Alaska).

[238] Also rock sheep, wild sheep, argali, and steppe sheep. There is no popular Russian name (except, apparently, "steppe sheep" for the Ustyurt form). Usually the animal is simply called a sheep; it is often called arkhar in Middle Asia. *The English common name is *argali*—Sci. Ed.

[239] Perhaps Ust'-Kamenogorsk, but not Semipalatinsk as some Soviet authors have stated (Lydekker, 1913).

[240] In Soviet as well as foreign literature even today Pallas is still cited as the author of the name *musimon* and the reference given as *Zoographia Rosso-Asiatica,* vol. 1, 1811, p. 230. Sardinia is cited as terra typica. Some misunderstanding has been created in this regard, evidently by Miller (1912). It is to be noted that Pallas in *Zoographia* described under the name *Aegoceros musimon* quite clearly the Turkmenian sheep which "lives with us" (in Russia, V.H.) only in the rocky mountains east of the Caspian Sea in Turkmenia, more often in Ceraunis mountains in Persia, and most probably far into the Asian mountains as well ("apud nos tantum in rupestribus montosis ad orientem maris caspii in ditione Turcomanorum occurrit, frequentius in

1841. *Ovis polii.* Blyth. *Proc. Zool. Soc. London,* 1840, p. 62. Pamir, Lake Zorkul'.[241]

1841. *Ovis gmelini.* Blyth. *Proc. Zool. Soc. London,* 1840, p. 69. Environs of Erzurum, Asia Minor.

1841. *Ovis vignei.* Blyth. *Proc. Zool. Soc. London,* 1840, p. 70. Astor, Kashmir.

1841. *Ovis ophion.* Blyth. *Proc. Zool. Soc. London,* 1840, p. 73. Cyprus.

1842. *Ovis cycloceros.* Hutton. *Calcutta journ. Nat. Hist.,* vol. 2, p. 514. Kandahar region ("Hazara hills"), Afghanistan.

1850. *Ovis arkal.* Eversmann. *Estestv. Istoriya Orenb. kraya* [Natural History of Orenburg Region], pt. 2, p. 271. Northern Ustyurt. 1852. *Ovis arkar.* Brandt. *Beitr. z. Kenntn. d. Russ. Reiches,* vol. 17, p. 310. Substitute for *arcal* Ev.

1873.[242] *Ovis karelini.* Severtsov. Vertik. i. gorizont. rasprostr. Turkest. zhivotnykh [Vertical and horizontal distribution of Turkestan animals]. *Izv. Obshch. Lyubit. Estestv., Antrop. i. Etnogr.,* vol. 8, no. 2, pp. 84 and 86; tab. 1. Trans-Ili Alatau between Ili and Issyk-Kul Rivers.

montibus Ceraunis Persiae, et verosimillime ulterius in montosa Asiae excurrit"). Pallas gave local names of the species used by Russians ("steppe sheep"), Turkmens, Persians, Khivans (arkal) and Indians. All this, as also his description, can leave no doubt whatsoever that his *Aegoceros musimon* was the Turkmenian sheep (*O. a. cycloceros* and *O. a. arkal*), and cannot be construed as *O. a. musimon* as done currently.

In fact, it has been pointed out in the text that the "Caspian animal from Sardinia and Corsica, which Cetti described quite well (loc. cit.), is no different" ("caspium animal a Sardo et Corsicano omnino non differt"). Among the references to much older literature given by Pallas, there is also a reference to Cetti and his description of Sardinian mammals and the Sardinian name "mouflon" (*Muflone*). Against the backdrop of this information however, this reference is inadequate for ascribing to the Sardinian form the description and name of Pallas. At the same time, it is also extremely undesirable to assign the name *musimon* to Turkmenian sheep. There is also no need for this since the name *musimon* had already been used (in 1782) by Schreber for the mouflon of the Mediterranean islands. A solution to this nomenclatural problem calls for more specialized studies. Attention is simply drawn here to the matter but no formal conclusions proposed, and the nomenclature of Turkmenian and Corsican-Sardinian forms has been maintained in accordance with tradition.

For information on the "Ceraunis" mountains in Persia (Iran), see Nasonov (1933, p. 44).

[241] The lake near which this species was found is called Zorkul' (the English sometimes called it "Lake Victoria") and not Serykul' as sometimes written (Nasonov, 1923; Tsalkin, 1951). Quite often, non-Russian authors, following Lydekker (1913), placed the type locality as "Pamir in the neighborhood of Syr-Darya" (!) Wood, who collected the type specimen, traveled in 1838 to the sources of the Amu-Darya (Oxus) and not the Syr-Darya.

[242] Published in 1872.

1873. *Ovis heinsii.* Severtsov. Ibid., pp. 84 and 87. Aleksandrov range, near Merke.[243]

1873. *Ovis nigrimontana.* Severtsov. Ibid., pp. 84 and 87. Karatau.

1873. *Ovis collium.* Severtsov. Ibid., p. 154. Chingiztau and Arkat mountains north of Balkhash.

1873. *Ovis argali* Pall. (a) *mongolica.* Severtsov. Ibid., p. 154. Eastern Mongolia and Trans-Baikal.

1873. *Ovis argali* (b) *altaica.* Severtsov. Ibid., p. 154. Altai.

1873. *Ovis argali dauricus.* Severtsov. Ibid., Table IV. Trans-Baikal.[244]

1898. *Ovis ammon typica.* Lydekker. *Wild Oxen, Sheep, and Goats,* p. 177. Altai.

1898. *Ovis poli typica.* Lydekker. *Wild Oxen, Sheep, and Goats,* p. 192. Pamir.

1898. *Ovis sairensis.* Lydekker. *Wild Oxen, Sheep, and Goats,* p. 185. Saur mountains within Dzhungaria.[245]

1902. *Ovis sairensis littledalei.* Lydekker. *Proc. Zool. Soc. London,* 1902, pt. 2, p. 83, pl. 7. On Ili River southeast of Kuldja; Tien Shan within China.

1905. *Ovis vignei varenzovi.* Satunin. *Zapiski Kavk.* Otd. I. *Russk. Geogr. Obshch.,* book XXV, vol. 3, p. 11. Kopet-Dag.

1913. *Ovis ammon humei.* Lydekker. *Catal. Hume Bequest.,* p. 6. Tien Shan, north of Kashgar.

1914. *Ovis polii karelini* forma *melanopyga.* Nasonov. *Izvestiya I. Akad. Nauk,* 1914, p. 699. Suuk-Tyube in Trans-Ili Alatau.

1914. *Ovis severtzovi.* Nasonov. Ibid., 1914, p. 761. Nuratau mountains, Kyzylkum.

1914. *Ovis vignei bocharensis.* Nasonov. Ibid., p. 1130. Bal'dzhuan on upper courses of Kyzylsu, right tributary of the Pyandzha.

609 1921. *Ovis ophion armeniana.* Nasonov. Izvestiya Ross. Akad. Nauk,1919, p. 1215. Vic. Bayazet (Bayazid) city in Turkey, south of Ararat.[246]

1923. *Ovis polii collium* forma *albula.* Nasonov. *Geogr. rasprostr.*

---

[243] "A skull of this sheep was found in the Tokmak district but with no precise indication of the place of the find; geographic distribution is not known. The grayish-brown argali sheep which Severtsov saw from a distance in the Aleksandrov mountain range, near Merke, probably belonged to this species" (pp. 97 and 98).

[244] A formal description of the form is not available and the name not even mentioned in the text. The name appears only in the caption to the colored illustration in Plate IV. Probably, this is simply another name for the form *mongolica* described in the text. Of it is stated—"Eastern Mongolia, primarily Trans-Baikal" (i.e., Dauria—V.H.) (Severtsov, 1873, p. 154).

[245] The author mentions the Saiar, Sair, and Jair mountains at 86° E long. and 47° N lat. This corresponds to the area cited.

[246] Not Armenia and Trans-Caucasus as often written.

gornykh baranov Starogo Sveta [Geographic Distribution of Mountain Sheep of the Old World], p. 82. Near Akmolinsk.

1923. *Ovis polii collium* forma *obscura.* Nasonov. Ibid., p. 82. Arkat mountains north of Balkhash.

1923. *Ovis ammon przevalskii.* Nasonov. Ibid., p. 118. Sailyugem range, eastern extremity of Altai.

1929. *Ovis polii nassonovi.* Laptev. *Opredelitel' mlekopit. Srednei Azii* [Guide to the Mammals of Middle Asia], p. 76. Talassk Alatau. (V.H.)

Diagnosis

Sheep of small, moderate, and large size, of fairly slender and light build. The color of the flanks and back is monochromatic or a large light-colored area appears on the upper part of the flanks. Sometimes a tress of long hair occurs on the neck and upper parts of the chest. The horns are extremely diverse in size and shape (heteronymous, homonymous, and perverted). Females sometimes bear horns and sometimes not.

The bony core of the horn in adult males is relatively long (length more than that of the basal circumference and greater than the maximum length of the skull). The skull is relatively long (width at posterior end of the orbits usually less than its height). The cranium is relatively short (length usually not more than 43% of the maximum length of the skull). The facial part is not shortened and the nasal bones are relatively long (over one-third the maximum length of the skull), with prominent depressions on the lacrimal bones. Geographic variation is high and the geographic range extensive. (V.H.)

Description[247]

The geographic variation of argali sheep is so great that there is no parallel to it among mammals and hardly even among vertebrates in general. The extreme forms of the geographic series of subspecies differ from each other in their general appearance and degree of development of individual characteristics more than in the vast majority of good species of ungulates. This feature makes it difficult to give a precise description. The characteristics given here are of individual features and the trend of their geographic variation for the species as a whole. Additional data are given while describing individual subspecies (see section "Geographic Variation").

---

[247] Literature on this species of mountain sheep is extensive. More complete and recent information on characteristics of Russian sheep have been given by Nasonov (1923 and other works) and Tsalkin (1951). The present description has been based mainly on the information contained in these works.

In spite of the occurrence of extremely divergent races, the general appearance of the animal throughout the range is almost identical. Argali sheep are handsome, slender animals of light build, standing on long thin legs, with small hooves, thin and elongated neck, a proportionate head with a prominent bulging nose and small ears. The horns impart an extremely characteristic appearance to argali sheep; they are usually large, bent beautifully in the form of a spiral, and sometimes large and heavy. They compel the animal to hold its head high, somewhat tilted backward, and impart to it a somewhat haughty bearing. In some forms a large and luxuriant tress of long hair occurs on the neck and chest, sometimes even on the throat. The tail is short and does not catch the eye. Argali sheep represent a cursorial type of animal and differ distinctly in general appearance from heavier, thick-legged goats. They have nothing in common even with domestic sheep. This is particularly true of the very large form of argali sheep inhabiting Middle Asia and the Altai.
610 Small forms with poorly developed horns (mouflon, *O. a. musimon*) and probably even Trans-Caucasian sheep (*O. a. gmelini**) are apparently somewhat less slender and more stocky.

Mountain sheep have a well-developed pelage differing from that of goats (*Capra*) in shorter length, lesser growth of underfur, and greater pneumatization of hair of the winter coat. Seasonal dimorphism is distinct; sex-related dimorphism in some forms is very marked. Four main types can be recognized based on coloration and characteristics of pelage. These types are strictly localized geographically but are connected with each other through intermediate forms.

I. Mouflon type. Predominant color of winter coat of males dark cinnamon with a slight admixture of lighter-colored hair. Sometimes it is rusty-cinnamon or blackish-brown. On the upper side of the flanks and on the back, on each side, a large light-colored patch of varying form, size, and color occurs. Sometimes it is very large, rises high onto the back, even joining the patch on the opposite side to form a large "saddle". Sometimes (more rarely) the patch is small and in the form of a small spot of light-colored hair on the side. Usually the patch is light-colored, sometimes pure or almost pure white, and stands out very sharply against the general dark background of the animal. Otherwise it is largely obscured by the hair of overall background color and quite faint. In rare instances the patch is not visible or almost invisible.

**O.a. gmelini,* Armenian urial—General Editor.

Abdomen, groin, inner surface of legs, tip of muzzle, and lower jaw white or whitish. Neck and upper part of head somewhat lighter-colored than trunk with a brownish shade. Upper part of legs has rich color of trunk while lower parts dirty white. Rear of thighs white, with white coloration rising fairly high and forming a small speculum around the dark upper portion of the tail. Hair on lower part of neck and chest somewhat elongated (up to 15 cm) and forms a small indistinct tress of cinnamon-black color. Usually tress does not reach the throat but, exceptionally, may reach corners of the lower jaw. Luxuriant beard absent. General shade of color of winter coat of females somewhat lighter, with no light-colored spots on the flanks and without hair tress.

Color of the summer coat of males lighter and brighter than the winter coat, rusty-cinnamon or rusty-yellow. A dark-colored belt runs along the back. Otherwise coloration features are the same as in winter coat. Summer color of females somewhat lighter than that of males.

This form is thus characterized by a very dark, rich color, with sharply contrasting well-formed spots, and poorly developed dark monochromatic dark tress of hair.

Such a color is characteristic of sheep of Corsica and Sardinia (*O. a. musimon*) and is not seen among native Russian populations. Acclimatized mouflon in Crimean preserve have this type of color.

II. Trans-Caucasian sheep type. Color scheme very similar to that of mouflon.

Main color of winter coat rusty-yellow, rusty-brown, or chestnut-rusty of different shades. White spots on flanks usually quite sharp and front and lower margins particularly prominent. Sometimes they are so much larger that they merge on the spine. Hair of dominant shade of trunk always mixed in with white hair of spots, and occasionally trunk hair is predominant over white. In this case lateral spots indistinct and area usually small. In some animals light-colored spots are almost nil and only a small admixture of white hair seen instead. Sometimes hair of trunk in front of white spots dark brown or even black. Such darkening occurs more often on the back.

Abdomen, inner and lower part of legs, rear of thighs ("speculum"), tip of muzzle, and lower jaw white or whitish. Head grayish-
611 brown or rusty-yellow. Tress well developed but variable in dimensions; color ranges from dark brown to cinnamon-brown. Length of hair of tress varies from 8.0 to 20 cm; hair toward chest

longer and darker. Tress generally commences 10 to 17 cm from base of head but lengthening of hair almost from base of head has been recorded.

Color of female winter coat somewhat lighter than that of males; light-colored spots and tress of hair absent.

Summer coat of males lighter than winter coat, light-colored spots absent, and tress very poorly developed, consisting sometimes of isolated tufts not more than 8.0 cm long, and somewhat darker in color than trunk. Summer coat of females similar to that of winter coat but slightly duller. Mane and spots on flanks absent in summer.

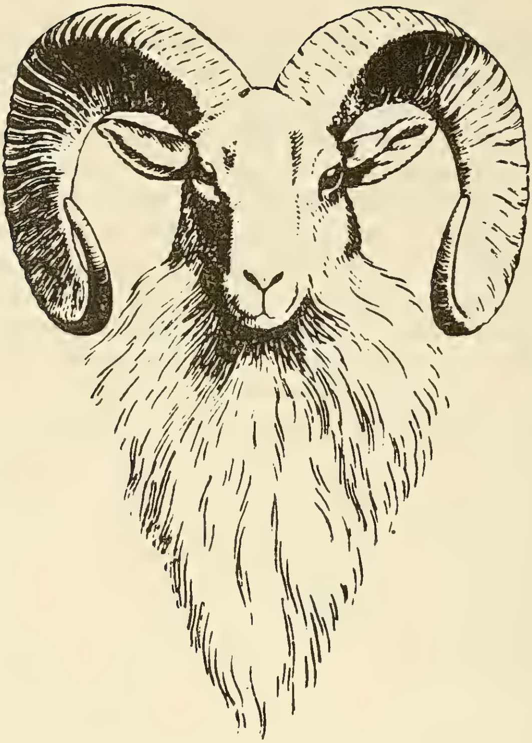
This type is thus characterized by a fairly light and bright general color, well-developed but usually vaguely contrasting lateral spots, and a small monotoned dark tress, similar to the one present in the preceding type. This type, in common parlance might well be referred to as "desert" mouflon with reference to coloration. Sheep of this type are found in Asia Minor and northwest Iran and, in the Soviet Union, Trans-Caucasus (*O. a. gmelini*).

III. Turkmenian sheep type. General color of trunk in winter sandy-yellow or cinnamon-yellow, sometimes lighter or even darker. No light-colored spots on flanks and color of trunk uniform.[248] Abdomen, thighs, inner surface of legs, tip of muzzle, and lower jaw white, sometimes with a slight darkening. Lower parts of legs dirty yellow or whitish. Rear of thighs white but "speculum" small and not very distinct. Color of flanks and abdomen sharply demarcated; at junction of the two sometimes a darker border zone, usually interrupted in the middle, occurs. Small light brown spot often present on posterior surface of ulnar joint.

Tress on throat and neck well developed, large, and luxuriant. Unlike the previous type, long hair here commences right at the base of the head in the form of two tufts on the sides joining posteriorly at the level of the larynx. They form a luxuriant "spade-shaped" beard or laterally spread jabot [ruffle], much wider than the head. This beard merges directly into the tress on the neck and upper portion of the chest. Length of hair of tress may reach 20 cm or more. Upper part of tress ("beard") consists of pure or dirty white 612 hair. Number of dark hairs in this region small but steadily increase posteriorly where they predominate over light-colored hair. Tress in old animals contrasting, beautiful, and rich. Young animals sport a dark-colored tress. Luxuriance and general level of development of

---

[248] Occasionally some light-colored hairs occur at the place where a light-colored spot occurs in animals of other races.



611 Fig. 212. Extreme growth of tress on throat and neck of mountain sheep, *O. a. "arkal"* in winter coat (from Nasonov, 1923). Sketch by N.N. Kondakov.

tress show individual variability and probably geographic variability sometimes.

In winter, coloration of females same as males but the former do not bear a tress.

Color of summer coat similar to winter coat but slightly lighter. Tress in males either not developed or only weakly developed, consisting only of elongated hair.[249]

This type is thus characterized by a light color, often of the "desert" type, absence of spots on the flanks, and a very large, luxuriant tress, the hair of which is particularly long and forms a large beard or jabot.

This type of color and tress is seen in sheep of Afghanistan, some parts of Iran and adjoining territories, in Turkmenia along the east coast of the Caspian Sea, and in the mountains along the right bank of the upper courses of the Amu-Darya and lower Pyandzha (*O. a. cycloceros* and *O. a. bocharensis*).

---

[249] Reports by some researchers that the tress is also developed in summer, albeit weakly, are probably based on an examination of hides of animals which had not fully molted. Quite possibly molt in this region is somewhat prolonged or the elongation of hair of the winter coat commences earlier.

IV. Pamir sheep type. Color of this type exhibits high individual variability. In the winter coat color of back and flanks varies from a dark and fairly bright cinnamon-brown to a light, rusty-cinnamon or pale brown. Between these two color types—dark and light—multiple transitional shades occur. For example, in some individuals a broad dark cinnamon-brown band occurs on the back and descends comparatively little onto the flanks; in others only a slight darkening on the back is apparent. In still other animals there is no darkening on the back, which is a uniform pale brown like the flanks. Color of the latter merges, usually very gradually and without sharp boundaries, into the light dirty or golden-yellow color of the abdomen and groins. Tail, zone around it, and rear of thigh, like the abdomen, yellowish-white. In dark-colored individuals light-colored area around tail fairly sharply demarcated from color of back; in light-colored individuals this transition is gradual. Color of head also varies greatly from dirty yellowish-gray to yellowish-brown. Forehead and occiput darker than rest of head, and brownish or cinnamon of different intensities. Upper part of extremities up to carpal joint and hock same color as trunk or slightly darker, a vivid brown or cinnamon shade. Below these joints legs dirty yellowish-white. Upper part of neck either almost the same color as the flanks or a very light yellowish-brown. Along the midline of the neck a narrow, faded brown region usually occurs. Below this the neck is a dirty yellowish-gray or yellowish-white. Long hairs form a small tress on lower part of neck and on chest (Tsalkin, 1951). Tress very poorly developed and occupies a small area down the neck and chest; hair short, not more than 8.0 to 10 cm. It has little in common with the rich tress characteristic of sheep of the preceding type, which is particularly well developed in the upper portion of the neck (beard or jabot).

Color of females in winter similar to that of light-colored males and hair on ventral part of chest not elongated. In summer both males and females sport a bright cinnamon-red coat.

This type of color and tress is characteristic of sheep of the Pamir-Alai mountains, Tien Shan, Kazakh *melkosopochnik,* and the Altai (*O. a. polii* and the related form, *O. a. ammon*).

In various parts of this region some deviations are seen in the general tone, intensity, degree of variability, and other features of coloration, but the overall general type remains the same. The characteristic features of this type are a rich and often fairly dark color, 613 absence of lateral spots, and very poorly developed or totally absent tress.

The four main types, based on color and development of tress, are readily differentiated. However, in certain territories (partly outside the USSR) they merge and the features of different types may combine.

The horns so characteristic of the general appearance of argali sheep constitute an important feature but are subject to considerable geographic variation. Many basic features of skull structure are associated with the horns and depending on their growth, concomitant changes in the skull are apparent. Horns serve as one of the most significant characters for taxonomic differentiation.

There are three main types of horns.[250] Two represent extreme variants and differ very sharply, while the third is somewhat intermediate. These main types and the individual variations within them characteristic of specific groups of races and individual races are highly localized geographically. All three types blend in the
614 characters of individual races and through forms of individual variability within the limits of individual races. This transition shows a definite geographic direction and occurs in a regular sequence. The development of characters proceeds from more primitive in the west to highly specialized in the east. Geographic variation is exhibited mainly in absolute and relative body size, weight and nature of curvature of horns (the two correlate), and nature of horn surface (edges and relief). The most primitive horn types are characteristic of Cyprus sheep (*O. a. ophion*), while Pamir (*O. a. polii*) and Altai (*O. a. ammon*) argali sheep are the most specialized.

The three main types of horns are observed in the following areas in the USSR.

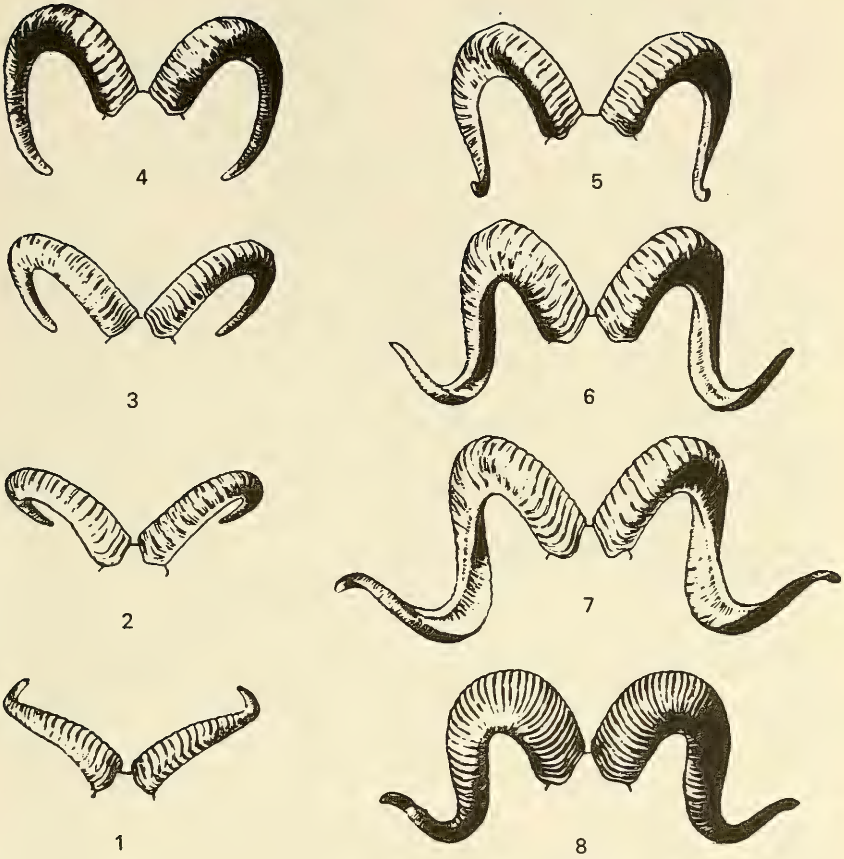
I. Trans-Caucasian sheep type (heteronymous horns). Horns of this type are characteristic of small races of sheep. They are relatively small (length along curvature usually not more than 70 cm,[251] and thin at the base. Frontal surface somewhat tapered outwardly, rib between frontal and outer-lateral (temporal) surfaces (outer rib) smooth, and general features of basal portion of horn gentle or somewhat rounded. Horns emerge from skull sideways and upward while terminal portions bend backward and inward (toward the neck to face each other); tips may bend somewhat upward (negative flexure).[252]

---

[250] Description applies only to fully grown adults and old animals.

[251] Additional horn measurements are given under the description of general measurements presented in the section "Geographic Variation".

[252] Different authors interpret differently terminology describing the flexure of



613 Fig. 213. Geographic variability and horn types of argali sheep, *Ovis ammon* L.

1—Trans-Caucasian sheep, *O. a. gmelini* (heteronymous horns, negative bend); 2—Urmian sheep, *O. a. urmiana* (perverted or flat horns, neutral bend); 3—Elburz sheep, *O. a. orientalis* (same as preceding); 4—Turkmenian sheep, *O. a. cycloceros* ("highly perverted"; commencement of positive bend); 5—Turkmenian sheep, *O. a. cycloceros* (homonymous horn, positive bend—predominant type of horns of this form; preceding [4] encountered rarely); 6—Tien Shan sheep, *O. a. karelini* (very distinct homonymous horn, positive bend); 7—Pamir sheep, *O. a. polii* (sharply expressed homonymous horn; extreme development of positive bend); 8—Altai sheep (argali), *O. a. ammon* (sharply expressed homonymous horn; extreme development of positive bend). Original drawing by N.N. Kondakov (based on material from Tsalkin, 1951, with modifications and additions). V.G. Heptner.

Individual variability seen in horns in which terminal portions tend to bend less sharply inward (and up). In such cases they do not meet opposite each other but are set more downward. The entire horn is flexed almost in a single plane. This tendency leads to the formation of horns of the second or perverted type.

Heteronymous horns in the Soviet Union are characteristic of only Trans-Caucasian sheep (*O. a. gmelini*). Outside the USSR they are seen in sheep of Asia Minor, some western parts of Iran, and particularly in sheep of Cyprus (*O. a. ophion*).

II. Urial or Bukhara sheep type (perverted horns). Horns of this type are a regular characteristic feature in small races of sheep (with a skull length of up to 260 mm). Only one form (*O. a. vignei*) from among moderate-sized races has such horns. In others this type is a rare individual variation.

A typical perverted horn proceeds upward and sideways from the skull and is crescent-shaped in a single plane or almost so. Its tip is directed down and inward toward the neck and does not turn upward nor bend outward, i.e., does not begin the second round of the spiral and does not have a positive curve at the tip. The lateral rib is smooth and the frontal surface usually tapers outward, bulging slightly. In cross section the horn base reveals smooth outlines and may even be slightly rounded. Typical perverted horns appear in some forms inhabiting the Middle East beyond the boundaries of the USSR (*O. a. isphaganica, O. a. urmiana, O. a. laristanica, O. a.*
615 *orientalis, O. a. blanfordi,* and *O. a. punjabensis*). They are also characteristic of mouflon (*O. a. musimon* of Corsica and Sardinia)[253]

---

horns of sheep (and other cavicorns). This is partly due to confusion or misunderstanding. In this work the terminology of N.V. Nasonov has been followed as it is commonly employed in Soviet literature, even though in some respects it is inferior to the terminology of Lydekker (1913). According to Lydekker a heteronymous bend is one which runs against the thread of a screw (corkscrew) and is characteristic of wild animals such as antelopes. The horns of all sheep, according to him, are homonymous (see diagnosis of horns—Lydekker, 1913), i.e., coiled in the direction of the thread of a screw. The types of horns described here, like similar horns in Caucasian tur (*C. cylindricornis*), Barbary wild sheep (*Ammotragus*), and blue sheep (*Pseudois*), are also regarded by him (and quite justifiably) as homonymous but of a special "perverted" type ("mathematical perverted").

Nasonov labeled horns of an altogether different type "perverted," keeping in view Lydekker's interpretation (1913, p. 143). Nasonov coined this term independent of Lydekker. Hence the statement by Tsalkin (1951) that Nasonov took the term and concept of perversion from Lydekker is based on a misunderstanding. This should be borne in mind to avoid the same error when referring to non-Soviet literature. In general, Soviet terminology for horn types has been needlessly complicated in recent years.

[253] In this case the geographic sequence of development of characteristics within

acclimatized in Crimean USSR. Yet other types of horns, often homonymous, even heteronymous, are not so rare in this type of sheep.

Within the USSR only two indigenous forms—Ladakh sheep (*O. a. vignei*) and Bukhara sheep (*O. a. bocharensis,* Tadzhikistan)—bear perverted horns. Some rare individuals among the latter have homonymous horns. Perverted horns occur rarely as an individual variation among Turkmenian sheep (*O. a. cycloceros*) generally characterized by homonymous horns. In this case the perverted horns have a flat frontal surface and a well developed anterolateral rib, retaining other horn characteristics typical of this race. Thus this type of horn is characteristic of sheep of the Middle East, more precisely, Iran-Afghanistan.

Perverted horns structurally constitute a transitional form between heteronymous and homonymous types and could well be designated heteronymous horns with the ends turned down. Perverted horns also link heteronymous and homonymous types through some individual variations, which acquire importance in some races as the main structural feature of the horn.

The transitional status of perverted horns is evident from the geographic distribution of subspecies with this type of horn. Such animals are generally found in areas lying between countries where heteronymous horns are developed (in the west) and those where sheep have homonymous horns (in the east).

Horns in which the ends are set forward are sometimes classified as "perverted". Such a structure is often seen, for example, in sheep of the Turkmenian-Khorasan region. However, this type should be designated homonymous, albeit at an earlier stage of development. When the end is set straight forward, essentially outward in relation to the main plane of the horn (bent positively), it commences the second round of the spiral.[254]

---

the species is disturbed. Heteronymous horns should be expected as the main type in mouflon, since they are the most western form.

[254] The term "perverted," if indeed necessary, is best applied to serpentine horns which are bent in a single plane. Overusage of the terms "perverted" and "perversion" results in confusion and ambiguity, especially when "highly" and "weakly" perverted are included (Tsalkin, 1951). A "highly perverted" horn is essentially one in the initial stage of a positive bend, i.e., a homonymous horn (or weakly homonymous horn) and hence no other name is suitable.

In general, the terminology of horns is extremely complicated. It would be simpler to term the horn bend in one single plane as in the crescent-shaped horns described above (true perverted horns according to Nasonov) as neutral, bending of the horn tip inward toward the neck as negative, and the outward bend away from the neck and head to the same side (right one to the right, left one to the left) as positive (both the latter definitions are fairly universal). Accordingly, one could use the terms positive,

III. Pamir sheep type (homonymous horn). Horns of this type are characteristic of all large and the largest races (*O. a. polii, O. a. ammon,* and related forms). They are exclusive in these forms and other horn types are not found even as individual variations. This type of horn is regularly seen in almost all races of moderate dimensions (*O. a. cycloceros* and related forms) but is not developed to the maximum extent. Even neutral (perverted) horns are found in some (*O. a. cycloceros*) as a rare individual variation.

The horn flexure is sharply positive—it turns upward, sideways, and backward, in the form of a fairly gentle lateral spiral, the right one to the right and the left one to the left (away from the body). 616 When developed maximally, the horn forms two complete twists of a spiral and the terminal part is directed directly to the side (*polii* group).

When this type of horn is minimally developed, its end is set forward or only slightly turned out and the horn only commences the second twist of the spiral (*O. a. cycloceros* and related forms). In this group the horns are much shorter in length, smaller in size, and less massive. Morphologically, horns of this type represent a transition from neutral (perverted) to a more complete positive (homonymous) type, and hence constitute a vital link in the chain of imperceptible transitions between the two extreme types.

Races with the most intense development of horns can be divided again into two types. In one (*polii* group) the horns are very long, slender, and with a relatively narrow base; the rib of the horn is usually well developed, the frontal surface flat, and the cross section triangular with fairly acute angles. In the other (*ammon* group) the horns are very short and massive, with a broad base in relative and absolute terms, the frontal surface slightly convex, the outer-lateral rib smoothed, and the cross section of the horn base triangular with extremely rounded corners.

Horns of this type may be very large (dimensions of both horns [together] greater than 160 cm) and massive (weight up to 30 kg or more).

Fully developed horns of this type are seen in sheep of the Pamir-Alai and Tien Shan mountain systems (*polii* group), the Altai, and the Central Asian mountains (*ammon* group), i.e., toward the easternmost part of the range of the species. Less prominent but wholly typical forms of this horn type are seen in sheep of Turkmenia,

---

negative, or neutral horn bends. The terms homonymous, heteronymous, and perverted are best avoided in view of divergent interpretations.

eastern parts of Iran and Afghanistan (*cycloceros* group), and the Kyzylkum (*O. a. severtzovi*).

It is important to note that this region, geographically, falls between the habitats of animals with neutral horn bends (perverted) and highly developed horns with a positive bend (homonymous).

In the overwhelming majority of races females have horns; mouflon (*O. a. musimon*) females are mostly without horns; Trans-Caucasian (*O. a. gmelini*) and Elburz (*O. a. orientalis*) females are either with or without horns; and Turkmenian (*O. a. cycloceros*) mostly bear horns but some do not. Thus the presence or absence of horns is subject to geographic variation.

Horns of females are very weak, thin, compressed from the sides, straight or slightly bent like a scimitar, set backward, and slightly sideways. Even when fully developed the length of female horns is not more than one-half the maximum length of male horns. In the diminutive races they are small (5.0 to 6.0 to 9.0 cm), somewhat larger in moderate-sized races (even to 25 to 30 cm), and largest in large races (35 cm). The maximum horn length in the largest form (*O. a. ammon*) is 53 cm. In general, however, the horns of females are somewhat proportionate to their size, whereas in males the relative increase is greater.

Horns of males undergo significant changes with age; the greater these changes the more complex the ultimate form of the horn and the greater its size. The spiral-shaped homonymous horns of large sheep undergo a long and complex course of development. Development is simpler in sheep with perverted horns bent in one plane. Such horns grow throughout the animal's life essentially in the same plane in which the young horn began growth. Horns of intensely homonymous types, for example in Pamir sheep, in the first few years go through perverted (flat) and weakly homonymous stages. Perverted horns sometimes tend (at the commencement of growth) to form a heteronymous (negative) bend. Thus stages corresponding to fully developed horns of other types can be seen in the growth of some individual horns. Horns of very young lambs are similar to those of females.

The skull of argali sheep has undergone wide geographic variability in overall size and some vital structural features. These variations are far greater than differences between different species of
617 many ungulates. A decisive factor in skull variability is the degree of development of the horns and of the bony core supporting these horns; differences in overall size of the animal play only a secondary role.

There are two main types of skull structure—western or mouflon type and eastern or argali type.[255]

The western or mouflon type is characterized by the following features. Skull small or moderate in size (maximum skull length not more than 300 mm); bony core relatively long but thin (base circumference about 60% of length); high point of forehead falls above orbits and somewhat to the rear; occipital region of skull projects backward considerably, beyond line of rear end of bases of bony cores; frontal relatively small and not sharply bent in vertical direction; parietal relatively large and forms a significant part of brain case behind horns; upper profile of skull behind the horns gentle and forms an acute angle with facial part of skull; supraoccipital greatly flexed and its squama forms with the base a distinct angle—squama turned up and forward and base down and forward or straight down; facial part of skull small, narrow, and relatively short (not more than 60% of maximum length of skull); premaxillae relatively short and usually do not wedge between maxilla and nasal; nasals comparatively short and narrow; intercalary bones rare between maxillae, nasals, and premaxillae; orbit relatively large; interpterygoid fossa narrow; articular surfaces of occipital condyles relatively small; and fusion of skull sutures incomplete and delayed.

The skull of the second or argali type is characterized by the following features. Measurements large (maximum length over 300 mm); bony cores relatively thick (base circumference over 70% of length); high point of forehead shifted back and falls behind orbit; roof of brain case behind horns inclined steeply (almost perpendicular) and angle which it forms with horizontal axis of skull approaches a right angle; squama and base of supraoccipital bone do not form an acute angle between themselves; their profile together with that of entire skull portion behind horns forms almost a straight line and occipital region of skull only slightly projects beyond line of rear end of bases of bony cores; frontal large and highly flexed in vertical plane; parietal small and forms a small part of brain case behind horns; facial part of skull high, broad, and long (length over 60% of maximum skull length); premaxilla large and its ascending process quite often falls between nasal and maxilla; intercalary bones often occur between nasals, maxillae, and premaxillae; nasal relatively broad and long; interpterygoid fossa broad; articular surfaces of occipital condyles large; and fusion of sutures, especially in dorsal part of skull, complete and occurs early.

Both skull types are distinctly localized geographically; skulls of the mouflon types are found in sheep which inhabit western parts of the range, i.e., islands of the Mediterranean Sea, Asia Minor, Iran, Afghanistan, Baluchistan, and northwest India; and in the USSR in the Trans-Caucasus, Turkmenia, Ustyurt, Kyzylkum, and the Pri-Amu-Darya part of Tadzhikistan.

---

[255] The characteristics of the two types given here are based on Tsalkin's work (1951).

Sheep of the argali type inhabit all the remaining areas, i.e., eastern part, Pamir-Alai and Tien Shan system, *melkosopochnik* of eastern Kazakhstan, and in the east up to the boundaries of the range of the species.

Thus the two types are not found together anywhere.

Moreover, the skulls of different races of the same group are not wholly identical, and within the limits of each type forms occur wherein the characteristic features of a given type are expressed very 618 sharply while in other animals they are not. Among the races of the mouflon type skull features are particularly sharp in the more western forms, i.e., Mediterranean (*ophion* and *musimon*) and partly Asia Minor and Iranian forms. Among the races of the argali type skull features are distinctly seen in groups of Pamir sheep *(O. a. polii)* and especially Altai sheep (*O. a. ammon*). It is significant that the mouflon group contains some forms with skulls exhibiting the salient features of the argali skull type. They occupy a somewhat intermediate position between the two groups. Their role as a connecting link is emphasized by the fact that these forms (*O. a. bocharensis,* Tadzhikistan; *O. a. cycloceros,* Turkmenia, northeastern Iran, and Afghanistan; *O. a. severtzovi,* Kyzylkum; and partly *O. a. nigrimontana,* Karatau) occupy an intermediate geographic position between the regions of the most typical development of both groups.

As mentioned earlier, the structural features which distinguish the two groups relate to the level of development of horns. Typical members of the mouflon group have absolutely and relatively small, weak, and light horns, while typical members of the argali group have absolutely and relatively large, massive, and heavy horns. Previously listed forms with a skull of intermediate structure possess horns of moderate size.

The skull of the eastern group (argali) compared with that of the western group is undoubtedly more specialized and could in this respect be considered progressive. The skull of adult members of the mouflon type is similar, in some features, to that of juvenile animals of the argali type. The skull of members of the latter group thus passes through the "mouflon" stage. To some extent the same is also true of intermediate forms (*cycloceros* and others). A similar phenomenon is also seen in the structure and development of horns (see above).

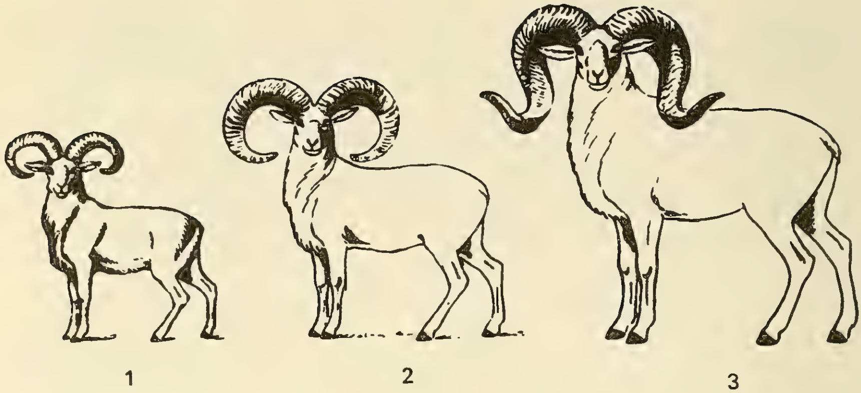


Fig. 214. Geographic variability of overall size of argali sheep, *Ovis ammon* L. 1—Trans-Caucasus sheep, *O. a. gmelini;* 2—Turkmenian sheep, *O. a. cycloceros;* 3—Altai sheep (argali), *O. a. ammon.* Sketch by N.N. Kondakov.

The general body size and weight show wide geographic variation, with no parallel among other mammals.[256] The size of males of the smallest forms inhabiting the USSR is as follows: Crimean mouflon (*O. a. musimon*)—body length 110 to 130 cm and height at withers 65 to 75 cm;[257] Trans-Caucasian sheep (*O. a. gmelini*)—body 619 length 130 to 148 cm, height at withers 77 to 94 cm, and chest 88 to 108 cm. The largest form (*O. a. ammon,* Altai) stands 125 cm at the withers while the Pamir-Tien-Shan form (*O. a. polii*) comes close at about 120 cm. The weight of the smallest forms of the species (*O. a. musimon*) is 25 to 50 kg, with an average of not more than 40 kg, while the largest weigh 200 kg or more. Thus individuals of the largest forms stand almost twice as high at the shoulders as those of the smallest, and in weight surpass them four to five times. Depending on the overall size characteristic of the different races, the size of newborn lambs varies greatly. Newborn lambs of Kopet-Dag sheep (*O. a. cycloceros,* a race of moderate dimensions) weigh around 2.5 kg, while those of the Tien Shan (large race) weigh 4.44 to 4.58 kg, i.e., almost a twofold difference.

Between these extreme forms there are several gradual, transitional forms or races of intermediate size. Thus the size of males of the Kopet-Dag race (*O. a. cycloceros*) is as follows (average): body length 140 cm, height at shoulders 94 cm, height at sacrum 99 cm, and gross weight 63 kg.

---

[256] Significant variations, but on a smaller scale, are seen in some deer in the archipelago of southeast Asia. It is remarkable that this very great range of variation is among the mainland races of sheep.

[257] Adequate data are not available for the European mainland mouflon and Crimean animals. The Cyprus form, smallest of the species (*O. a. ophion*) measures about 65 to 70 cm at the withers.

In general, all the races can be divided into three groups which are well localized geographically: a group of small races in the west, a group of large ones in the east, and a group of races of moderate dimensions in the region in between (Iran-Afghanistan and Turkmenia; see below for comments on skull measurements).

The difference between individual subspecies, though readily discernible in size, is often smoothed out because size is not only age-related but subject to individual variability. As a rule, forms that are close systematically, usually geographically neighboring, exhibit quite broad overlap. This is particularly true of weight. This characteristic shows extreme individual variation, depending not only on age but also on season; gross weight increases greatly toward the period of rut in autumn and falls sharply by the middle and end of winter when the animals are often emaciated. Usually Kopet-Dag male sheep from January to March are no heavier than 78 to 80 kg, but individuals killed in October have weighed 85 to 96 kg. Females weighing no more than 41 to 46 kg from January to March may weigh 56 kg in autumn.

Size difference between the two sexes is clearly expressed—females are invariably smaller than males but not to the same extent in all geographic forms. Difference in size is evidently more in much larger forms than in small ones. The ratio of sizes in the moderate-sized Kopet-Dag form is as follows: general body length of males averages 140 cm and of females 127 cm, height at withers 94 and 81 cm, and height at sacrum 99 and 85 cm respectively. The weight of males averages 63 kg and of females 36 kg, i.e., about 57% of the weight of males. In the large Tien Shan forms the weight of males is almost double that of females.

The range of age-related difference in size is very great in view of continuing growth over a very long period. The growth rate however decreases gradually, if not for the whole, for at least much of the life span of the animal. In Kopet-Dag sheep increase in size has been traced up through seven years of age. The most perceptible increase of mass is reflected in body weight. Variations in mean measurements and weight of Kopet-Dag sheep are shown in Table 5 (Tsalkin, 1951).

620 The difference between newborn and old animals also reflects the amplitude of age-related variability. In argali sheep this range is very great, being greater in large races than in races of moderate size (data are not available for diminutive races). Thus the weight of

TABLE. 5. AVERAGE BODY MEASUREMENTS AND WEIGHT OF MALES

Age in years	Body length	Height at withers	Height at sacrum	Gross weight
1	104	72	76	21.0
2	120	84	88	34.0
3	131	91	95	42.0
4	136	93	96	52.0
5	140	96	99	60.0
6	142	95	100	65.0
7	144	95	99.5	78.0

Kopet-Dag sheep by the time they attain full growth increases 29 times (2.5 to 80 kg) and in Tien Shan sheep 40 times (4.5 to 180 kg) or probably even more.

Skull measurements reflect extreme geographic variation. In males of the smallest forms living within the USSR, i.e., acclimatized mouflon (*O. a. musimon*), the average maximum length of skull is 233 mm,[258] which in the smallest of autochthonous Trans-Caucasian sheep (*O. a. gmelini*) is 251 mm. In the largest Altai forms (*O. a. ammon*) it is 360 mm, which is 1.5 times the size of the smallest form. Between these extreme values several intermediate sizes occur.

All the various races of the species can be divided into three natural groups based on skull size. These groups are well localized geographically. The group of small races (maximum length of skull up to 260 mm) is represented by nine or ten forms distributed in the west (Corsica, Sardinia, Cyprus, Asia Minor, Iran, part of northwest India, and Tadzhikistan—*ophion, gmelini, laristanica, orientalis, punjabensis,* and others). The group of large forms (maximum skull length over 300 mm) is distributed in the east (Pamir-Alai and Tien Shan system and farther to the east) and consists of nine forms (*polii* group and *ammon* group). The third group, comprising moderate-sized forms (maximum length of skull 260 to 300 mm), is distributed in the intervening region, often in close proximity and overlapping the peripheral eastern forms of the western group (Baluchistan, Afghanistan, eastern Iran, Turkmenia, Ustyurt, and Kyzylkum). It includes three or four forms (*vignei, cycloceros,* and *severtzovi*). Thus in skull size argali sheep divide into the same three groups,

[258] In *O. a. ophion* from Cyprus it is about 225 mm.

also similarly localized geographically, with the same territorial mixing and overlap of features as in the polarities of several other characters of the group. Skull size may serve as an additional index to overall dimensions of the animal discussed above (further details of skull mesurements are given in the section "Geographic Variation").

The length of skull of females in each race is much smaller than that of males and average 216 mm in mouflon, 231 mm in the Trans-Caucasian form, and 318 mm in Altai sheep. In small forms the dimorphism of this feature is less discernible than in large forms. In mouflon and Trans-Caucasian sheep the skull length of females averages 92.0 to 92.5% of that of males, and in Altai sheep 88.5%.

The size and weight of horns in the different races vary greatly. It is significant that their relative increase from minimal to maximal sizes is not proportional to the quantitative increase of other dimensional features and is much greater. In fact, this increase is far from comparable even with geographic changes in overall size and weight. In the smallest of forms inhabiting the USSR horns reach 67 cm in length (rarely more) and the base circumference is 22 to 27 cm (average 24 cm; Trans-Caucasian sheep), or up to 75 cm in length with a base circumference of about 20 to 23 cm (average 21.5 cm; mouflon). These horns are relatively short and thin. In the largest of the Russian races and, in general, in the various races of the species as a whole, horn length reaches 190 cm with a base circumference of 35 to 40, average 37 cm (Pamir sheep, *O. a. polii*), or 125 cm length with a base circumference of 40 to 50 cm, average 44 cm (Altai sheep, *O. a. ammon*). The length of these gigantic horns is thrice that of the smallest horns, this proportion being twofold for the base circumference. The increase is 12-fold in mass (gross body weight increases only four or five times). The distance between horn tips in Pamir sheep may reach 1.5 m or more while the horn weight in Altai sheep may exceed 30 kg. The horn weight in Tien Shan sheep may constitute up to 8.0% gross body weight and is nearly equal to the
621 weight of the entire skeleton. Even larger horns are sported by Altai and Pamir sheep. A series of forms occupy intermediate positions between the foregoing extremes.

All the races may be divided according to horn size into the very same three groups defined on the basis of skull size: a western group with relatively small horns, eastern with very large horns (Pamir-Alai mountains, Tien Shan, and farther to the east—groups *polii* and *ammon*), and an intermediate group with horns of moderate size (Afghanistan, eastern Iran, Turkmenia, Ustyurt, and Kyzylkum—

O. a. cycloceros and contiguous forms).[259] (V.H.)

Taxonomy

In spite of its diversity, *O. ammon* as broadly interpreted here, represents a distinctly isolated species. There are no connecting links between it and the other species of the genus, i.e., snow [bighorn] sheep (*O. canadensis*). The easternmost forms of argali sheep (*ammon* group), although possessing some features characteristic of bighorn sheep, are nevertheless distinctly isolated from them in specific diagnostic features. It is significant that all researchers, including those who interpret the species *ammon* very broadly, have separated it completely from *canadensis* and no attempts to combine the two species are known.

The systematic affinities of the two species of the genus are difficult to judge, primarily because of the extreme diversity of features in the different races of *O. ammon*. There is no doubt that the two species are quite closely related. Nevertheless, the species as a whole should be regarded as less specialized than bighorn sheep.

Although a large number of forms of the species *O. ammon* are no less specialized, and in some respects even more specialized, than forms of *O. canadensis* (greatly shortened occipital region, large body size, horn size, etc.), extremely primitive forms are also found in the species *O. ammon*. Such is the case with respect to all the western races of sheep with moderate and small overall size and horns with a neutral (flat, perverted) and even negative flexure (heteronymous). The latter type of horn is characteristic of forms which occupy a somewhat intermediate position between sheep (*Ovis*) and goats (*Capra*), i.e., Barbary wild sheep (*Ammotragus lervia*) and blue sheep (*Pseudois nayaur*), and even some goats, for example, Dagestan tur (*Capra cyclindricornis*).

The geographic variation of bighorn sheep is also fairly wide but the magnitude of variability is not comparable with that of argali sheep. What is more important is that it concerns only secondary characteristics; the species as a whole in its main features is essentially monotypic. It is significant that even the extreme variants cannot be considered primitive or progressive, because all are variations of a single type. This type is extremely specialized and corresponds generally to the more specialized type of argali sheep (*ammon* group). In particular the horns of bighorn sheep occur only as the most specialized form, with a fully realized positive flexure

---

[259] For horn dimensions of females, see p. 894.

(homonymous). Bighorn sheep may evidently be considered a terminal link in the series running from more primitive goats (*Capra*) through intermediate forms between goats and sheep, and primitive forms of argali sheep (*O. a. ophion*) to specialized argali sheep (groups *polii* and *ammon*). Thus, bighorn sheep become the most specialized forms of the tribe, subfamily, and family. (V.H.)

Geographic Distribution

Argali sheep occur in Corsica, Sardinia, and Cyprus; mountains of the Near East (except the Arabian Peninsula),* Middle and Central Asia to the Trans-Caucasus, Kazakhstan and southern Siberia in the north, to the Himalayas in the south, and to Tabaishan (Shensi) and the Great Khingan in the east.

622 *Geographic Range in the Soviet Union*

The range in the Soviet Union (reconstructed) is quite extensive and constitutes a substantial part of the distribution of the species. It includes the southern montane parts of the Soviet Union—the Trans-Caucasus, mountains of Middle Asia and Kazakhstan, and part of southern Siberia and Trans-Baikaliya.

Because of its association with mountains and rugged topography, the distribution of the argali sheep has an extremely complex and irregular contour. Moreover, distribution is not continuous but broken into separate sections corresponding to individual mountain massifs or ranges, or to areas with a montane relief. These sections are sometimes totally isolated from each other, such an isolation being the result of some natural factors. Moreover, the ecological relationships of these sheep are such that under certain conditions they do not avoid regions with very low absolute heights, sometimes living even at sea level, and are capable of migrating from one elevated section to another, even across plains. This occurs at some places even during seasonal migrations and is not the result of straying. In their natural environment, i.e., without human interference, the actual isolation of individual populations in several instances is not complete, and distribution in some parts is actually less broken up than might appear at first sight.[260]

---

*Since reported from Oman; see Harrison, D.L., 1972. *The mammals of Arabia,* Vol. III, E. Benn, London—Sci. Ed.

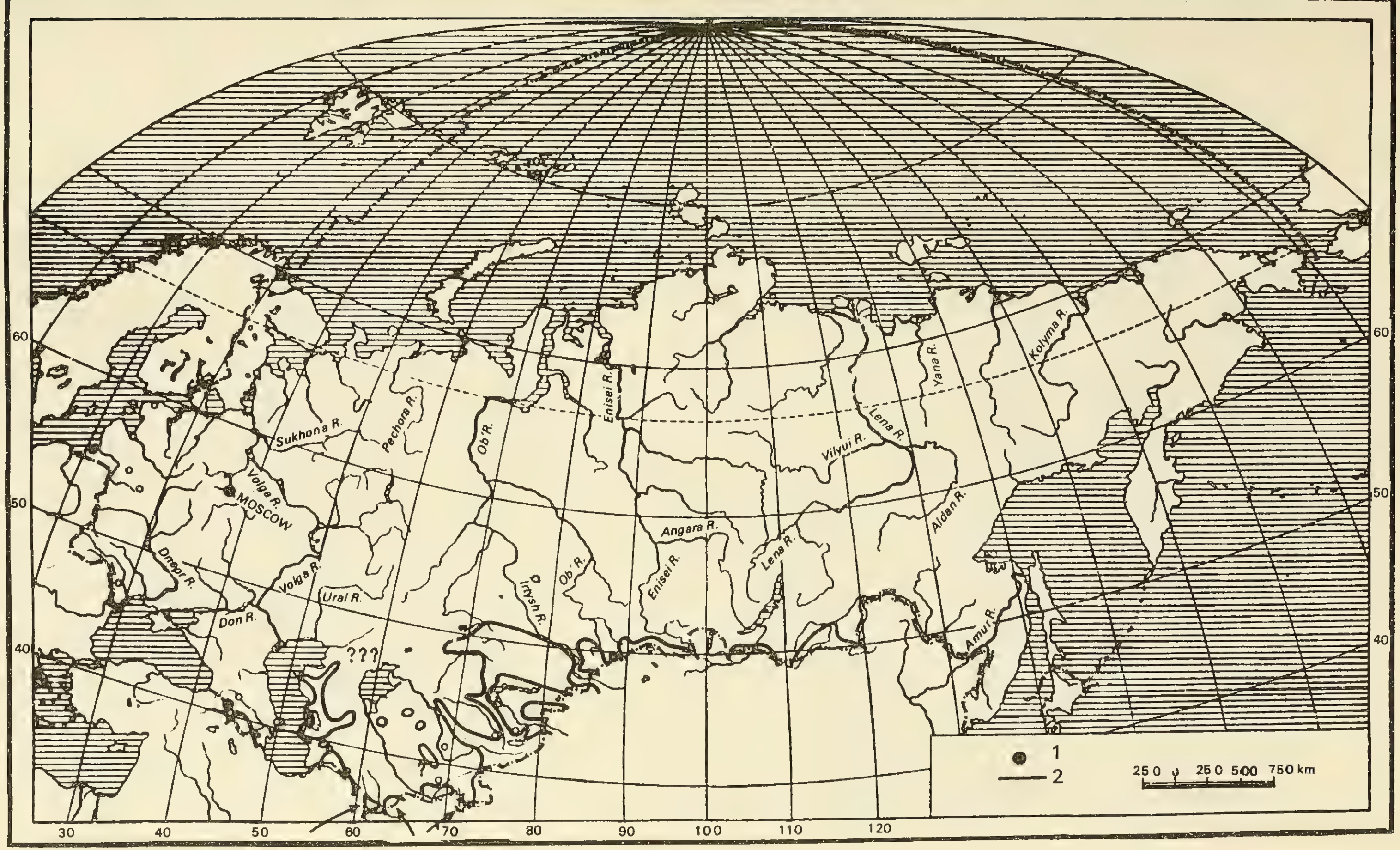
[260] For example, the populations of the Kopet-Dag, Balkhans, Caspian Sea coast, Mangyshlak, Ustyurt Chinks (see below), and some others.

However, even from very early times, and more so in more recent time, and the present, the range of argali sheep on the whole and particularly in certain areas has been exposed to very adverse human intervention. Total extinction of some small isolated populations surviving in environments where they were readily accessible has also occurred, for example on low and small montane sections within the desert (Kyzylkum). All possible migrations from one massif to another have been cut off by the establishment of human settlements, cultivated fields, destruction of the animals, etc. Thus, populations which were formerly in contact with each other have become totally isolated artificially, as for example the population inhabiting the Great Balkhan from that in Kopet-Dag.

In large massifs with a considerable range of altitudes almost everywhere, these animals were exposed to direct persecution or displacement, mainly by cattle, and have disappeared from the lower and middle zones, and survive only in the high mountains, often because of displacement from lower levels. This leads to isolation, or intensification of isolation, of even large sections of the habitat. Distribution, once fairly continuous and extending over a large area of the montane country, is now broken into individual, isolated, high-altitude sections and small isolated populations. Most races of argali sheep are not by nature high-altitude animals, preferring moderate and even low montane zones. In such cases where they have been displaced into the high mountains, therefore, the animals have undergone a secondary and purely artificial modification into high mountain animals. Such factors have determined the fragmentation of the present distribution, its dynamics at present, and its future.

Within the USSR the range is divided into two main parts—Trans-Caucasian and Middle Asiatic-Siberian—which are contiguous in the south, beyond the borders of the Soviet Union.

In the Trans-Caucasus the present-day distribution (animals of the *ophion* type) occupy a very small area south of the central Trans-Caucasus. The Araks River forms the southern boundary in the region from the mouth of the Azat River (directly south of Yerevan and slightly west of Artashat), and to Ordubad and Megra in the extreme south of the southern bend of the river. The northern boundary forms an arc between the above extreme points, through Mikoyan on the Arpachai and the upper reaches of the Nakhichevanchai at a distance apparently of not more than 50 to 70 km from Araks. Thus the range encompasses the montane district skirted by the Araks, especially the Sarai-Bulag range (spur of the South-
624 Gokchin range extending along the Vedi-chai and south of it), Daralagez (West-Daralaga) range, southern part of the Zangezur and


60
50
40
60
50
40
Kolyma R.
Yana R.
Lena R.
Vilyui R.
Aldan R.
Amur R.
Lena R.
Angara R.
Enisei R.
Enisei R.
Ob' R.
Ob' R.
Irtysh R.
Pechora R.
Sukhona R.
Volga R.
MOSCOW
Volga R.
Ural R.
Dnepr R.
Don R.
???
1
2
250 0 250 500 750 km
30
40
50
60
70
80
90
100
110
120

623 Fig. 215. Reconstructed range of argali sheep, *Ovis ammon* L. in the Soviet Union (scale in km).

1—former occurrence in Aragats (Alagez) massif; 2—boundary of range. V.G. Heptner.

Negram ranges, and the slopes and spurs of these and other associated mountains skirted by the Araks. The normal, fairly permanent region of settlement of sheep is deep inside the mountains, away from the Araks, but during migrations and seasonal movements (in winter) they are seen very close to the Araks (Negram mountains at Dzhul'fa) and in the Araks valley (at Dzhul'fa, Ararat, and Ordubad; Nasonov, 1923; Vereshchagin, 1947; Sarkisov, 1944; Dal', 1954; Dinnik, 1910).

In recent years the distribution outlined above has probably shrunk even more. In the past it was apparently wider but there is no direct evidence of this. The animals have been sighted on Alagez, at least in its western or northwestern parts (Mastara; Nasonov, 1923).[261]

The Middle Asian-Siberian region of the habitat of argali sheep is likewise split into many sections. West of the Amu-Darya and Aral Sea these sheep (*cycloceros* type) were dispersed fairly extensively. The range (reconstructed) covered all of the Kopet-Dag including Kyuren-Dag in the northwest, i.e., the last of the northwestern offshoots of Kopet-Dag lying south of Kazandzhik railway station. In this mountainous country distribution extended in the east up to the meridian of Artyk station where the mountains have already passed beyond the borders of the USSR. In the Kopet-Dag, south of this line, the habitation of sheep reached almost everywhere up to the state border or beyond it.

Farther on the range encompassed the Little and Great Balkhans, the shore of Krasnovodsk Bay and the upland district of Kuba-Dag lying north of Krasnovodsk. Farther north the range extended along the eastern and part of the northern shore of Kara-Bogaz-Gol and farther north along the western Chink of Ustyurt on Mangyshlak. Here the range included the Karatau and Aktau mountains to the northwest right up to Mangyshlak Bay, the Buzachi Peninsula, the precipitous region of the saline lake (former gulf) Kaidak, and Mertvyi [Dead] Kultuk, primarily its southern coast.

Apparently, from the above places in the region of Mertvyi Kultuk the range extended farther northeast in the form of a narrow strip and later eastward along the northern Chink of Ustyurt and probably reached even to the Aral Sea.[262] Sheep are absent in the interior of Ustyurt. From the slightly elevated and rugged regions on the east shore of Kara-Bogaz-Gol and the western Ustyurt Chink the range ran in the form of a narrow strip along the southern Chink quite far eastward. The occurrence of argali sheep in this area has been established, especially at Kazakhla salt lake, on the meridian of the western extremity of the Assak-Audansk basin (100 km to the south); the animals also dispersed along the Chink even farther eastward (V.P. Kostin).

---

[261] Doubts have been expressed about this information (Sarkisov, 1944) since it is not substantiated.

[262] Information about distribution in this region is extremely vague. According to some old data, presented in a very general manner, sheep were distributed along "Tumansk mountains" (i.e., northern Ustyurt Chink) fairly widely and reached the Aral Sea. This distribution has also been accepted by Nasonov (1923). According to

At the latitude of the southeastern corner of Kara-Bogaz-Gol, at suitable locations, argali from Kara-Bogaz-Gol penetrated east toward the Karakum almost to Chagyl well (60 to 80 km east of the shore of the bay) and were encountered there at several places (A.K. Rustamov).

The occurrence of argali sheep in the Pri-Caspian district along the Ustyurt Chink is all the more significant since the animals lived there in an environment of typical and extremely severe desert conditions and at extremely low altitudes, at sea level and even below it (coastal cliffs of Kara-Bogaz-Gol and Caspian Sea).

The habitation of sheep in Kopet-Dag represents the northern part of the range covering eastern Iran and Afghanistan. Distribution north of Kopet-Dag, up to the northern Ustyurt Chink, at present an extremely tentative link, in the past was without doubt
625 completely effective and substantial. This is supported by taxonomic affinities of the corresponding forms (Kopet-Dag and Mangyshlak, see below).

At present (1950's) sheep have already disappeared from the Little Balkhan and are almost extinct in the Great Balkhan, and are totally absent in the region of Krasnovodsk Bay and north of Krasnovodsk. Likewise they are absent along the northern Ustyurt Chink although still sighted at Mangyshlak in far smaller numbers and in a reduced area. In the direction of the northern Ustyurt Chink argali sheep in recent times has extended only to the village of Kyzyl-Tas at Mertvyi Kultuk (E. Strautman, 1953). Along the southern and western Ustyurt Chinks, the eastern coast of Kara-Bogaz-Gol, and the region between Chagyl and Kara-Bogaz-Gol, these sheep are still encountered.

The area of distribution of these sheep in the Kopet-Dag has also undergone a significant reduction. The habitat throughout the range has shifted slightly from the region of foothills and low alti-

---

other data, especially recent material (E.I. Strautman, 1953; Bazhanov, 1951; Tsalkin, 1951), no confirmation could be obtained of the past habitation of argali sheep along northern Chink. These sheep are absent there today.

tudes to the much higher mountainous areas southward. Especially significant is the withdrawal from the western part of the range. Here sheep are already absent west of the Syunt and Khossar-Dag uplands lying above Sumbar, slightly east of Kara-Kal. These sheep are also absent between Sumbar and Chandyr. Their main habitations here are parts of the mountain range associated with the Dushak massif.[263]

These sheep are absent and were never present in the expanse between the Artyk (see above) in Kopet-Dag and the Tedzhen within the USSR since habitats in these regions are unfavorable for them (plains). A small isolated pocket of sheep occurs in southern Turkmenia in the Gyaz'-Gyadyk uplands along the right bank of the upper course of the Tedzhen. The Tedzhen forms the western boundary of the range in the stretch from the Afghan border (Zyul'faqar [Zulfikar] Pass) roughly up to Pul'-i-khatum (at 36° N lat.) or slightly more southward. The eastern boundary is formed by a line commencing from the above points on the Tedzhen River and extending for not more than 20 to 25 km away from the river. This small section of the range is in the form of an extension emerging to the west from Khorasan.

A narrow projection of the range extending east in the form of a small area of habitation of sheep along the Er-oilan-duz lake basin and along the gorge (ravine) of Kyzyl-Dzhar at the center of the Badkhiz (interfluve of the Tedzhen and Kushka)[264] merges with the Gyaz'-Gyadyk section.

A small isolated section of habitation, separated from the one described above and representing the extreme northern edge of the Afghan part of the range, covers the hills between the Kushka and the upper Murgab (Chengurets mountains; Heptner, 1956). Sheep in this area occur mainly along the southern higher regions of the interfluve and the range does not reach the confluence of the Kushka and the Murgab. East of the Murgab sheep are often sighted but apparently not regularly on the Karabil' upland located on the Afghan boundary, at a distance of 100 to 120 km east of Takhta-

---

[263] The distribution of sheep in the region under description, unless otherwise stated, is based on information from Nasonov (1923) and Tsalkin (1951) and original and compiled data from V.G. Heptner.

[264] The occurrence of sheep in the Er-oilan-duz basin is highly significant not only because the animals occupy torrid deserts with a severe climate and are almost without water, but also because they live not along the higher but along the low relief. Badkhiz is a gently undulating desert rising to a height of 500 to 700 m. Immense, and at places, almost vertical argillaceous walls arise from the lake basin and the Kyzyl-Dzhar gorge (Heptner, 1949 and 1956).

Bazar. Farther on, toward the Amu-Darya, sheep are absent.

The past distribution of sheep in southern Turkmenia in the expanse between the Tedzhen and Amu-Darya, as far as can be judged from the natural conditions of the country, was evidently the same as at present. Old information about occurrence in the region of Sarakhs and Mary is erroneous.[265]

626 In the region between the Amu-Darya and Syr-Darya, i.e., in the Pamir-Alai system, and in the remnant uplands to the north in Kyzylkum, the distribution of these sheep is extremely complex because of complex orography and landscape conditions. Moreover, the range at places underwent secondary changes quite early. Finally there is no adequate information about the distribution of sheep in this region.[266]

In the territory under discussion there are three main areas of occurrence of sheep, evidently isolated or almost isolated from each other. Each, in turn, is further divided into a few small sections. The first region (sheep of urial type, *O. a. vignei*) occupies the small montane areas adjoining the Pyandzha and its tributaries. The southern and in part the eastern boundaries of this section is represented by the Pyandzha, to which the range extends in places (Karatau mountains, Kafirnigan mouth and others). In the east the range extends at least to the Kulyab and the mountains lying between the Kyzylsu and Pyandzha; sheep are absent in Darvaza, however.

The northward extent of occurrence is poorly known. In the east these animals reach Bal'dzhuan in the north and, farther west probably northern Babatag; it is doubtful that they reach the latitude of Stalinabad [Dushanbe]. In the west the range encompasses all of Kugitangtau.[267] It is possible that the range extends in the north into the southern extremity of Baisun mountain [Baisuntau] lying north of Kugitangtau (a general reference to Baisun region is available; Flerov, 1935). The occurrence of sheep has been positively established in the north but only to the west and southwest of Ak-Rabat, lying in a large tract from Guzar to Shirabad roughly along the middle of this course (15 km northwest of Derbent; O.P. Bogdanov). Sheep are absent a little farther north, in the Sangardak-Darya basin covering the midportion of the massif (flowing into the Surkhan-Darya at Denau) (V.G. Heptner) as also on the western slopes of Baisuntau in the Guzar region (Lyangar; Salikhbaev, 1939). They are also absent throughout the Tupalang basin (flowing into the Surkhan-Darya above Denau at Sary-Assiya; Levinev, 1939), i.e., in the northern part of Baisuntau and thus along a significant part of the southern slope of the western extremity of the Gissar range.[268] There are no concrete and accurate references to the occurrence of these sheep in other parts of the Gissar range and this system apparently does not fall within the range.

---

[265] The range in eastern Turkmenia is based on original and compiled data from V.G. Heptner.

[266] Information is mostly superficial; reliable information is generally absent or only very old and unverified data are available for large regions. Moreover, material in some primary sources has been reinterpreted by recent investigators rather incorrectly. Therefore, some data from these compilations, extensively quoted, do not correspond to reality, or constitute oversimplification. Consequently, the boundaries of distribution of sheep in this territory, given here in a very general way, differ significantly from those usually given. New information on the distribution of argali sheep is extremely scanty.

[267] According to Nasonov, 1923; Flerov, 1953; Gureev, 1937.

The question of distribution and even the occurrence of argali sheep in the Zeravshan range is unclear. Evidently, at least in the past, they did live at places in this mountain range. It is significant, however, that so far there is only one concrete reference (Fedchenko) for the 1870's. This reference has been cited and somewhat supple-
627 mented by N.A. Severtsov (1873),[269] probably based on information provided by a traveler. Unfortunately, these data are extremely scanty and too vague to be reliable and no new data have appeared for almost 90 years. In any case, these sheep are absent at present in the extreme western parts of the Zeravshan range at Takhta-Karach Pass, south of Samarkand, roughly at its meridian and west of it (R.N. Meklenburtsev). All this compels one to leave open the question of the occurrence of sheep in this range.[270] Taking into consideration as well the information given above for the Baisuntau and Gissar range, the available literature on the distribution of argali sheep in these parts of Middle Asia should be treated circumspectly

---

[268] Argali sheep are also not known to occur in the southwestern part of the Gissar range in the region of the sources of Kashka-Darya (Meklenburtsev, 1958).

[269] Fedchenko's report (see 1950 edition) reads as follows: " . . . in Zeravshan mountains, mountain sheep . . . *Ovis vignei* species are found (p. 328). In Pendzhikent . . . I was given mountain sheep (*Ovis vignei*) which hunters found in the hills. . . in the course of the summer, even in Samarkand, I received an excellent male (p. 92). Males and females of *Ovis vignei* Blyth were obtained from Pendzhikent residents who shot them in the mountains along Zeravshan" (p. 100). N.A. Severtsov (1873) reports that Fedchenko's sheep "were found in the upper courses of the Zeravshan" (pp. 162 and 163) and that "*M. vignei* climbed, in summer, to the permanent snow line, i.e., even at Zeravshan to a height of 14,000 feet" (p. 217). It is Severtsov and not Fedchenko who emphasizes the occurrence on "the upper courses of the Zeravshan"; Severtsov's later report clearly pertains to data from Fedchenko and not to his own observations, as is sometimes reported (Flerov, 1935).

[270] It is significant that argali sheep are apparently absent also in the western parts of the Alai range as also in the Trans-Alai (see below).

and applied only in very general terms.[271]

The Pamir represents the second main region of occurrence of sheep in the expanse between the Amu-Darya and Syr-Darya. There sheep (*polii* type) inhabit the eastern part of the country. In the north they inhabit the Trans-Alai range but to what extent distribution extends west and whether it reaches the western extremity of the mountain range is not clearly known. They are most common, in any case, in the eastern part and evidently the range there is bounded by it. South of the Trans-Alai range argali sheep are present throughout the eastern Pamir. Westward their range is demarcated by a line running south through Fedchenko glacier, Tash-Kurgan on the Murgab River, the region of Lake Yashil'kul' and the passes Koi-tezek, Kok-bai, and Mats, and sources of the Shakhdara (Kala-i-Dzhushangoz) at the mouth of the Vakhan-Darya on the Pamir River (Nasonov, 1923; Flerov, 1935; Rozanov, 1935; Meklenburtsev, 1936).

Sheep are absent in the western Pamir, i.e., in Darvaza, Shungnan, and Roshan, with its high rocky ranges and extremely rugged topography. However, there is an altogether isolated, very small pocket of sheep (*vignei* type) within the USSR in the extreme southwestern corner of the western Pamir in Ishkashim and Vakhan [Wakhan] (Nasonov, 1923). Sheep are absent in the Peter the Great range.

In the Alai valley, in the eastern part, sheep occur extensively at higher altitudes (Irkeshtam, sections adjoining Kyzylart [Pass] and Bar-Doba, and others) and more rarely in the central part, where they are seen only in winter when they descend the mountain slopes (Kuznetsov, 1937 and 1948; Andrushko, 1955). They are evidently absent or rare in the western part of the valley (Daraut-Kurgan).

In the Alai range, argali sheep occupy only the extreme eastern part, in the Gul'chi district and southeast of it, and the mountainous part extending (from the east) toward Osh. How far the distribution of these sheep extends westward is not known, but they are not found in the Isfairamsaya and Shakhimardana regions, or at Kara-Kazyk Pass (south of the city of Ferghana) on the main axis of the range, or along the northern slope of it (V.G. Heptner).[272]

---

[271] "Tadzhikistan, from the right bank of the Amu-Darya River in the west [?—V.G.], to Darvaza in the east and Zeravshan in the north" (Tsalkin, 1951). "In Tadzhikistan all the montane areas of the north up to Zeravshan . . ." (Flerov, 1935).

[272] During his travels in 1871 Fedchenko did not once hear of mountain sheep in the Kokand Khanate in the course of his route of march on the northern slope of the Alai range in the expanse between Gul'chi and Isfara (roughly on the meridian of Kokand), nor while crossing the range in leaving Daraut-Kurgan in the Alai valley.

A third, fairly extensive and extremely characteristic part of the range of argali sheep (*O. a. severtzovi*) in the interfluve of the Amu-Darya and Syr-Darya lies in Kyzylkum and Nuratau range. The whole of the latter (height up to 2,160 m above sea level) and the small Aktau range adjoining Nuratau from the south form part of the range. There are references to the occurrence of sheep only at some points in the Kyzylkum on some isolated upland outliers in the desert with heights of not more than 1,000 and even 500 m. These are Sultan-Uizdag near the Amu-Darya southeast of Nukus at 42°, the Bukantau mountains, and to the southeast, the Tamdytau upland and adjacent Aktau.

628 Probably argali sheep lived even in other outliers of the Kyzylkum at altitudes up to only 600 to 700 m (Kosshony, southwest of Tamdy, or the upland near Dzhingil'dy, slightly to the south), but no data are available to support this. Quite probably sheep reached northward to the Kuvan-Darya in Kyzylkum (Nasonov, 1923; Meklenburtsev, 1937).

Sheep have now been extirpated from the Sultan-Uizdag and Aktau hills lying south of Nuratau (O.P. Bogdanov). In Nuratau itself sheep are encountered nowadays only in the western part (Meklenburtsev, 1937). No information is available relating to other uplands but they are probably absent in them or on the verge of extinction.

The places of occurrence of these sheep in the Turkestan range are geographically closely associated (through Nuratau) with the Kyzylkum area of the range and comprises a part of it. Information in this regard however is meager, very inconclusive, and somewhat contradictory. Quite possibly, in the past these sheep, at least in the western part of the range, were distributed fairly extensively. However, at present they are known only from the northern slope (foothills) southwest of Ura-Tyube; even at the beginning of the 1940's they were apparently rare (V.B. Dubinin, 1954). They are absent slightly more to the east, in the region of Shakhristan. They are also presently absent in the Mal'guzartau mountains (R.N. Meklenburstsev), an offshoot of the Turkestan range toward Nuratau. No doubt, they formerly inhabited this area. Evidently the affinities of sheep living (or which lived) there are closer to those of Kyzylkum (*O. a. severtzovi*) than to those of Tadzhikistan (*vignei*) group.

Argali sheep are extensively distributed in the wide expanse north of the Ferghana valley bounded on the west by the Syr-Darya and on

According to him sheep were absent in the region he traversed (Fedchenko, 1950, p. 328). Evidently they were present at that time only east of Gul'chi.

the east by the Ili River and comprising the Tien Shan montane system (Tien Shan part of the range). However, their distribution in this area is quite complex and extremely uneven since argali sheep throughout their range avoid intensely rugged as well as forest regions and are confined to terrain of highland drainages.[273] In several places the range has evidently undergone significant secondary changes (extinction).

In the northwest the distribution covers the entire Karatau-range up to its northwestern extremity, the Karamurun mountains (height only about 300 m above mean sea level), the Boroldai mountains adjoining the Karatau from the southeast, the Kirgiz (Aleksandrov) range, Talas Alatau, and the adjoining northeastern extremity of the Ugam range (region of Aksu-Dzheboglin preserve), the Susamyrtau, mountains lying to the east of the Talas range and connecting it with the Dzhumgal and Kavak mountain ranges. In the region east of the meridian of Lake Son-Kul' and the eastern extremity of the above ranges and south of Issyk-Kul, argali sheep occur in several areas and occupy essentially all of this expanse in the east up to the state border (Kokshaal mountain system), in the northest to the region of the Khan-Tengri massif, and in the north to Tersk Alatau inclusive. In the south, the distribution covers the Atbasha range and the region of Lake Chatyrkel'. Through these sites along the moutains surrounding the Ferghana valley to the east, the Tien Shan part of the range, though mainly outside the USSR (continuation of the Kokshaal—the Koktun mountains), joins the Pamir-Alai section.

North of Issyk-Kul the range enters the Kungei Alatau, Trans-Ili Alatau, and Chu-Ili mountains. The range extends along them to the north and northwest over a long distance, reaching the small elevations of Dzhambul, Chagarla, and Baigar, and continuing even into the Bet-Pak-Dala desert north of the southwestern extremity of [Lake] Balkhash. The northernmost habitat of argali sheep in this region is the shore of Kara-Kamyz Bay, on the west shore of the lake, and Kogashik village west of Balkhash, roughly at 46° N lat. and 70° E long. in the desert plains. In the Bet-Pak-Dala desert and at Balkhash the area of distribution almost joins with that part of the range 629
which occupies the Kazakh *melkosopochnik* in the north (see

---

[273] Our ideas, usually oversimplified, on the distribution of argali sheep in Tien Shan require reexamination. In any case, the widely prevailing and usually accepted view about the occurrence of this animal throughout this mountain system is erroneous. Only a schematic outline of its distribution in the Tien Shan system is given here, drawn from a review of factual data.

below). It is certain that in the past there was contact (movement back and forth) between these two regions. According to some data (A.A. Sludskii) it is so here even now.

The Ketman' range on the left bank of Ili also falls within the distribution.[274]

Argali sheep are apparently absent in much of the Ugam range (except the northeastern extremity), in the Pskem, Chatkal' and Kuramin ranges, in the Uzunakhmat range approaching the northeastern extremity of the Chatkal' from the southeast, and in the Ferghana, at least the southern slope and southern offshoots (Isfadzhailyai, Isfatau, Baubashata, and some others). Thus the species under description did not occur over a fairly significant part of the southwestern section of Tien Shan system within the USSR.[275] It is difficult to say whether the absence of this animal dates back to antiquity or is of recent origin.

The range has now shrunk at several places in the Tien Shan system. Thus argali sheep are no longer seen in the northwestern part of the Karatau.

East of the Ili a significant part of the habitation of these sheep (*polii* type) lies in the Dzhungar Alatau. The range in this region covers not only more elevated montane sections, but also the foothills and *melkosopochnik* surrounding them to the south, southwest, and west, as well as north, for example north of Kopal and north of Taldy-Kurgan. At present the occupied area in this section has somewhat shrunk at the periphery. The range also encompasses the Tarbagatai and Saur and the small uplands associated with them, for example the Sartologoi plateau north of the Tarbagatai (Antipin, 1941).

Sheep (*polii* type) occupy a very significant expanse in eastern Kazakhstan to the north of the latitude of Balkhash. They are distributed very unevenly and the range consists of small pockets, related to more elevated areas in the eastern Kazakhstan hill country attaining absolute heights of up to 1,000 m or even less, in rare cases up to 1,500 m (Kyzylrai), and a very rugged montane topography. Thus the range includes the uplands Del'begetei, Arkat, Chingiztau, Kokon', Dogalan, Urdatau, Kyzylrai, Ortau, Aktau, Al'dzhan, Enrikei, Kandygetei, Kentskie mountains, the upland regions of Dzhanark in the Sary-ark district (Mungly, Arkarly, and Kyzyltau), Ulutau,

---

[274] The range in this part of Tien Shan has been drawn from Nasonov, 1923; N.A. Severtsov, 1873; Kuznetsov, 1948 and 1948a; E.I. Strautman, 1953; Shnitnikov, 1936; Antipin, 1941 and 1947; F.D. Shaposhnikov, 1956; Kashkarov, 1927; Beloslyudov, 1948; and others.

[275] Negative data from a series of faunistic studies.

Bayan-Aul' mountains, Kokchetav mountains in the Kersakpai steppe, the entire Karkaralinsk district and some others (Kuznetsov, 1948; Antipin, 1941; Nasonov, 1923; Tsalkin, 1951, Selevin, 1924, 1925, and 1928; N.A. Severtsov, 1873; Beloslyudov, 1948). To the east sheep are also found in the Kalbin Altai.

The peripheral points limiting the range of argali sheep in the west are the Ulutau mountains, the uplands slightly southward in the Karsakpai district, and Ortau mountains near Akmolinsk.[276] The northern boundary runs from Akmolinsk to Bayan-Aul and from there toward the uplands slightly south of Semipalatinsk (Del'begetei mountains). The Irtysh (Kalbin Altai) forms the eastern boundary. The southern boundary runs from Karsakpai through the upper course of the Sarysu (Zhana-Arkin region), later descends south and runs along the southern edge of the Kazakh *melkosopochnik* at a distance of a few tens of kilometers from the northern shore of Balkhash. Thus, northwest of the western extremity of Balkhash the boundary traverses Arkarly and Kyzyltau villages ("mountains"), lies on the parallel of the Mointa railway station, but 80 to 130 km to the west of it (Aktau and Ortau mountains, sometimes shown as the southern boundary of distribution in this area, fall slightly more to the north). Roughly along this line the [southern] boundary of the range runs to the Tarbagatai, the Chingiztau remaining slightly to the north.

630 Argali sheep undoubtedly occupied all of this region and regular contact occurred between populations of more elevated and rugged regions. Extensive contact likewise took place with the range of the sheep in Chu-Ili mountains (see above).

Argali sheep are already absent today in some pockets within the region outlined above. In the Bayan-Aul mountains they were exterminated by 1918. It is impossible to cite here all the areas of the present-day occurrence in the region under description. Sheep are sighted, or were until recently, in quite a large number of places, for example the Ulutau, Chingiztau, Arkat, Ortau, Kyzyltau, and other mountains. The most important home of these sheep is the Karkaralinsk mountains (Kyzylrai and adjoining areas).

An isolated pocket of argali sheep (*ammon* type) within the USSR, separate from the Irtysh River region described above, occurs in the Altai-Sayan system. This region, representing the northern edge of the Central Asian part of the range of the species, is very small and split into a few, often isolated sections.

[276] In highland portions of the Kokchetav and Borov regions argali sheep were apparently absent; at least there is no information about their existence there.

In the western Altai the range covers the Kurchum and Narym ranges, the mountains along the Bukhtarma and probably the Ul'bin, Ivanov, and Ubin ranges. In the west the distribution in this region extends to Ust-Kamengorsk and to the place Kvasnyi Yar, slightly below along the Irtysh.[277] To the northeast and east of the above places the range encompasses the Tigerets range and apparently even the Korgon plateau lying southeast of it, where are found the source of the Charysh, and the Koksa, a tributary of the Katun. The range also includes the region of the upper reaches of the Katun, the Katun Alps and reaches the Uimon. Based on the foregoing, the range may be taken as covering the Kokui, Kholzun, and Listvyag ranges also.

In the extreme south the range encompasses the region of the sources of the right tributary of the upper Katun, i.e., the Argut, places along the Dzhaster, and the Ukok plateau (basin of Ak-Alakha River), and the Sailyugem range.[278] Farther on the range includes the Chuya steppe, i.e., the upland region at the sources of the Chuya River lying between the Sailyugem, southern and northern Chuya, and Kurai ranges and the Chikhachev range. The distribution here extends even up to the passes in the Bashkaus basin.[279] To the east, beyond the Chikhachev range, the habitat of sheep covers the upland region of Mongun-Taiga where Lake Kyndykty-Kul' and the sources of the rivers flowing south into Lake Achit-Nur (Mogen-Muren River) and Ureg-Nur (Kargy River) are located. In the north the range extends only for a short distance, encompassing the plateau of Lake Dzhulu-Kul,' from which the Chulyshman flows, and the southern extremity of Shapshal range—on the north to the west only to the source of the right tributary of the Chulyshman, the Shavla, and to the east, the source of the Kemchik. Argali sheep are absent in the central and northern parts of the Shapshal (Yanushevich, 1952; V.G. Heptner).[280]

---

[277] The occurrence of argali sheep in the western part of the Altai is quite difficult to explain since the animal has not been reported in most places for over 100 to 150 years. Information for that period is very scanty. Thus occurrences in the Ul'bin, Ivanov, and Ubin ranges have not been reported and the assumption is based on finds along the Bukhtarma, Ust-Kamenogorsk, and eastward.

[278] There is no information for the southern Altai ranges and the Tarbagatai at the sources of the Bukhtarma (on the western side of the Ukok), but they should probably be included in the range of argali sheep.

[279] According to data of Nasonov, 1923; N.A. Severtsov, 1873; Kolosov, 1938 and 1939.

[280] In the map given by Nasonov (1923) the position of the Sailyugem and the habitat of argali (*O. a. ammon*) designated by the number "XXVII" are altogether incorrect and give a false impression of the penetration of the species north. The

In the Tuva region the range of these sheep extends in the form of a narrow strip all along the Tannu-Ola—both Western and Eastern—and also includes the Sangilen range to the east. Their occurrence in so-called East Tuva uplands, i.e., basins of the sources of the Bol'shoi (Biya-Khem) and Malyi (Ka-Khem) Yenisey has not been established (Nasonov, 1923; Yanushevich, 1952).

631 Throughout the whole of the region under description to the east of the Irtysh these sheep are encountered quite regularly, albeit in small numbers, in Chuya steppe (not north of Kosh-Agach), in Mongun-Taiga and the southern Shapshal, and along the Tannu-Ola and Sangilen. They were extinct in western Altai quite long ago, even at the end of the eighteenth and early nineteenth century.

Throughout the expanse of the Western and Eastern Sayans argali sheep are absent and were evidently never present in the period under discussion.[281]

An isolated pocket of argali sheep occurred within the USSR in Trans-Baikaliya. It occupied the extreme southern part of the country and represented the northern extremity of the eastern Mongolian part of the range of the species. At present sheep are absent throughout Trans-Baikaliya; they disappeared at the end of the eighteenth and in the first half and even in the middle of the last century. The latest information about them pertains to the 1850's. The map of their distribution had to be reconstructed on the basis of extremely scanty data.[282]

The Trans-Baikal habitation of sheep was apparently divided into two isolated parts within the USSR. The western section comprised the moutains along the Dzhida, probably south of it. Animals were sighted at Tsagan-Ussui village on the Dzhida River. This section extended in the east at least to the mouth of the Dzhida on the Selenga. Sheep were known to occur at Ust-Kyakhta on the Selenga. It is possible that in the western Trans-Baikal steppe and xerophilous region sheep were somewhat more widespread.

---

number "XXVII", placed just around the latitude of Minusinsk, should be brought down to 50° N lat.

[281] The reference to a capture of the animal at the source of the Chekhan River (V.N. Skalon, 1936) on the northern slope of the Western Sayan (northern source of the Kantegir, about 52°20′ north), assuming the report to be true, could only be an exceptionally rare transgression of the animal far beyond its range (see data above for the Shapshal). Evidently information about finds of sheep at the sources is also erroneous or pertains to an exceptionally rare occurrence (Nukhu-Daban; Nasonov, 1923).

[282] Distribution in Trans-Baikaliya, unless otherwise stated, is mainly based on data from Nasonov (1923) and the original sources cited by him.

The second section of the distribution of argali sheep lay in southeastern Trans-Baikaliya. In this section the animals were sighted in the extreme south at the sources of the Onon and Chikoi (Bal'dzhikan region), along the Onon, in the montane region between the Onon and Ingoda (Onon-Cholon mountains along the left bank of the Onon), and in the region between the Onon and Argun in the extreme south from Borzya on the Soktui and Abagaitui up to the state border (Tutkhalui, Chir, and Soktui mountains). In the north their occurrence was reported not only along the Onon but also along the lower Ingoda (Galkino), 50 km in a straight line from the mouth of the Ingoda, and evidently in the upper reaches of the Shilka (reckoning from the confluence of the Ingoda and Onon) (Maak, 1859). Finally, sheep were reported even in other similar areas such as the Onon-Cholon "steppe mountains of Russian Dauria, i.e., Russian part of the Amur peaks" (N.A. Severtsov, 1873).

The above sightings fall in a triangle which includes the southwestern part of the Borshchovochnyi range on the left bank of the Onon, more precisely the Onon range, and perhaps part of the Daurian range, the expanse between the lower reaches of the Ingoda and Onon (Aga basin) and the region of the lowermost reaches of the Ingoda and the upper reaches of the Shilka. East of the Onon the range included the Erman, Argun, Klichkin, Nerchin, and the western part of the Gazimur ranges up to the upper reaches of the Shilka. These are the only ranges in which conditions accord completely with the ecological requirements of the argali, and are an integral part of the arid steppes and semidesert of southeastern Trans-Baikal. Between these two areas of distribution of argali sheep lies a significant expanse of montane taiga in Trans-Baikaliya.[283]

As was said, argali sheep have long been absent throughout Trans-Baikaliya. However, in 1918 a sheep was killed on the border in the mountains south of Mangut village in the upper reaches of the Onon (A.A. Nasimovich). Assuming this report to be correct, it 632 had to be an extremely rare intrusion from eastern Mongolia. These sheep had disappeared east of the meridian of Ulan-Bator even at the beginning of the first decade of the twentieth century (Bannikov, 1954).

[283] Repeated references in literature, even recently, to the occurrence of mountain sheep in the Yablonovyi range are based on some misunderstanding and are erroneous (see the chapter on snow sheep). In Trans-Baikaliya sheep were present only in the places mentioned above.

Geographic Range outside the Soviet Union

The range outside the Soviet Union includes Corsica, Sardinia, and Cyprus, the southern montane regions of Asia Minor (Taurus and Antitaurus system) south of the Solyanyi [salt] desert (sheep are absent in Pontic range and its western extension), mountains throughout Iran from the Elburz in the north to the Laristan mountains in the south, all of Afghanistan, mountains of Baluchistan, the Sulaiman mountains and the Salt Range in northwest India, the Himalayas eastward to Sikkim, Ladakh and the Karakoram, Tibet except the southeastern corner (region of sources of large rivers except Hwang Ho) and evidently the Trans-Himalayas and Tan-la system and eastern parts of the Kunlun, Altyntagh and Nan Shan systems, the mountains of the Alashan, Ordos, and southern Shensi (Tapa Shan range, around 110° E long.—easternmost point of habitation of the species), mountains of Inner Mongolia (Yabarai, Hara-Narin-Ula, and Muni-Ula, i.e., Datsinshan and Suma-Khada), southern half of the Great Khingan (roughly up to 46°30′ N lat., i.e., the watershed of the Nunni and Khalkhin-Gol, the most northeastern point of the range), montane regions of Kashgariya and Dzhungaria, the mountains of Mongolia-Khangai system, Altain-Nuru, Mongolian and Gobi Altai, and Khentei. At some places, for example in Khentei, these sheep have already become extinct.

These sheep (mouflon, form *O. a. musimon*) were acclimatized in Germany, Switzerland, Holland, Luxembourg, Italy, Poland, Czechoslovakia, Hungary, Yugoslavia, Rumania, and montane parts of Crimea (Crimean preserve—see below). (V.H.)

Geographic Variation

As mentioned earlier, mountain sheep exhibit extremely wide geographic variation, unparalleled among mammals. Hence authors of monographs (Lydekker, 1913; Nasonov, 1923) and articles right up to the 1940's identified several independent species of sheep. The author of the first monograph on this group,[284] N.A. Severtsov (1873), even divided sheep into two genera—western *Musimon* (mouflon group) and eastern true sheep *Ovis* (argali group). Seven species were recognized in the former and five in the latter (argali group; in this genus Severtsov placed three additional species of bighorn), i.e., 12 species in all. Lydekker (1898) recognized 7 species with 11 subspecies. These taxonomic divisions are now only of historic interest.

---

[284] Here and subsequently the discussion pertains only to the *O. ammon* group, i.e., Eurasian sheep excluding the snow sheep [bighorn] *O. canadensis.*

In the present century views on the composition of the groups have undergone radical changes. Lydekker (1913) recognized five species (*O. musimon, O. orientalis, O. laristanica, O. vignei,* and *O. ammon*). Nasonov's views underwent changes over several years and resulted (1923) finally in the recognition of eight species (*O. ophion, O. musimon, O. gmelini, O. laristanica, O. vignei, O. orientalis, O. polii,* and *O. ammon*). Of these, five were recognized as autochthonous species in the USSR—*O. ophion, O. vignei, O. orientalis, O. polii,* and *O. ammon.*

The formation of new ideas on geographic variation and structure of species has impelled many researchers in the last decade to merge species to a greater extent than was done by Lydekker. Thus Flerov (1932) recognized for the USSR only two species (*O. orientalis* and *O. ammon*), Bogolyubskii adopted three species (*O. musimon, O. laristanica,* and *O. ammon*), while others listed four (*O. musimon, O. ophion, O. orientalis,* and *O. ammon*; Bobrinskii, 1944). The view accepted here, i.e., one species of sheep in Eurasia in the east up to Mongolia, was established only in the 1950's in the works of some scientists who independently drew identical conclusions (Tsalkin, 1951; Kesper, 1952*; Haltenorth and Trenze, 1956*). However, even in the 1950's quite a few species were recognized by some authors (four species; Ellerman and Morrison-Scott, 1951).

633 The number of subspecies listed by different taxonomists continues to vary. According to Lydekker (1913) there are 23; Nasonov (1923) 29, of which 14 are found in the USSR; Tsalkin (1951) 24, of which 11 are Russian; and Ellerman and Morrison-Scott (1951) 32. In the present work ten autochthonous forms and an acclimatized one have been recognized for the USSR. It is probable that the autochthonous forms number only seven.

The following autochthonous subspecies inhabit the USSR.[285]

A. Group *ophion*—Cyprus sheep

1. Trans-Caucasian sheep, *O. a. gmelini* Blyth, 1840 (syn. *armeniana*).

Sheep of moderate size. Height at withers in adult animals 88 to 94 cm, maximum length of skull in males 246 to 264 mm (M 251) and in females 222 to 238 mm (M 231).

---

*Not in Literature Cited—Sci. Ed.

[285] The morphological features of the races are mainly drawn from Tsalkin (1951) with some modifications. All data pertain to adult animals. For more details of coloration, horns, and other features, see the section "Description".

Horns with negative bend (heteronymous), exceptionally sometimes bent almost in one plane (weakly perverted). Horn length up to 67 cm, rarely slightly more, and base circumference 22 to 27 cm (M 24). Frontal surface of horns tapers outward somewhat; outer ridge variously developed, usually indistinct. Females with or without horns.

Color varies from reddish-rusty to rusty-cinnamon; light-colored patch of varying size usually seen on sides of males. Chest and lower parts with small tress of elongated dark-colored hair not reaching up to throat and lower jaw.

Found in Trans-Caucasus. Outside the USSR seen in Turkey and northwest Iran, including the mountains surrounding Lake Urmia and south of Tabriz.

B. Group *vignei*—Urial

2. Ladakh sheep, *O. a. vignei* Blyth, 1840.

Sheep of moderate size but larger than the preceding form. Maximum skull length in males 257 to 272 mm (M 263). Facial part relatively long (58.0 to 62.5% of maximum skull length).

Anteronasal profile quite highly flexed and skull portion behind horns with relatively elevated profile.

Horns bent almost in one plane (slightly perverted). Frontal surface of horn tapers outward significantly; outer rib variously developed but usually smooth. Temporal and frontal regions relatively convex. Transverse knobs on horns relatively large.

General body color rusty-cinnamon; light-colored spots on sides absent. Tress on chest and neck better developed and forms something of a beard on throat and angles of lower jaw.

Found in Wakhan and Ishkashim (southwesternmost corner of the Pamir). Outside the USSR seen in mountains along the upper Indus, Ladakh, and Kashmir.

Information about the occurrence of this form inside the USSR is fairly old and requires verification. Recent literature contains no mention of Ishkashim and Wakhan sheep.

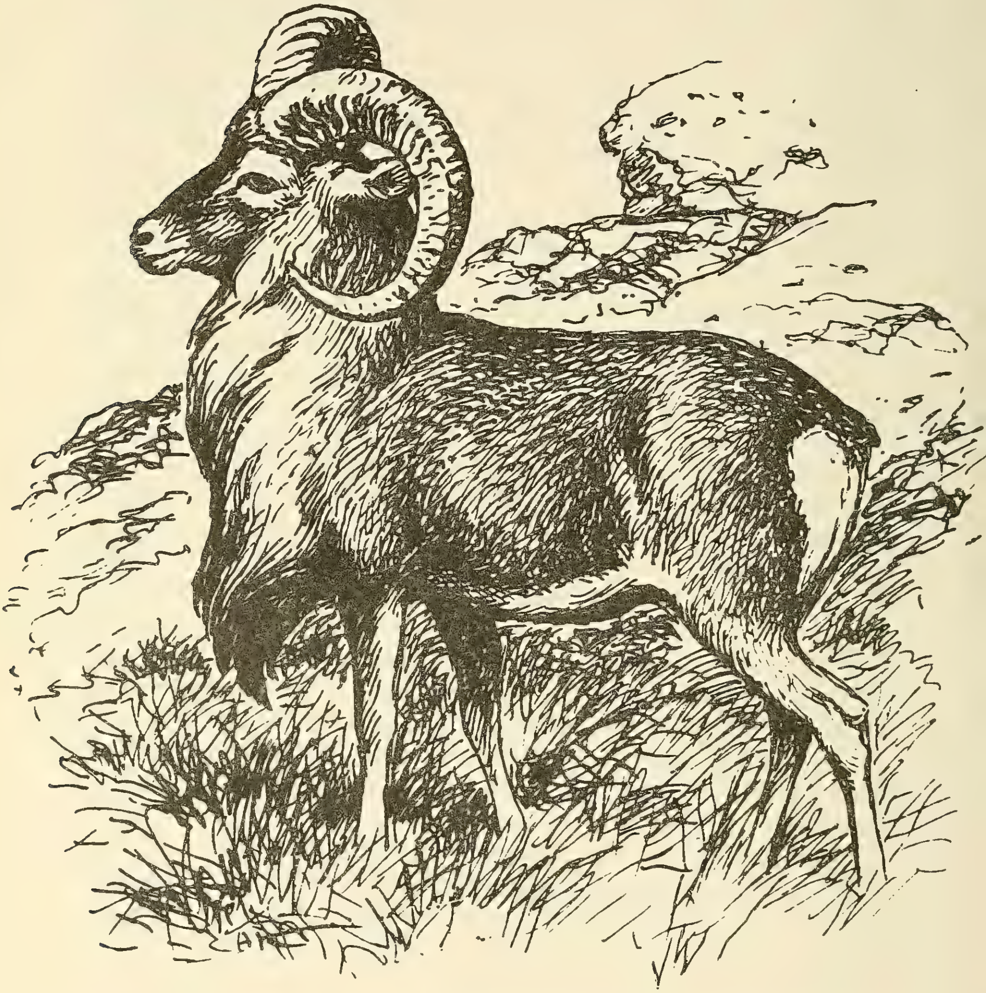
3. Bukhara sheep, *O. a. bocharensis* Nasonov, 1914.

Sheep of moderate size but smaller than the preceding form. Maximum skull length in males 232 to 255 mm (M 246) and in females 218 to 240 mm (M 224).

Flexure of horns variable but usually bent in one plane or close to it (perverted horns). Sometimes positive flexure seen (homonymous horn). Outer rib quite faint and transverse folds small. Horn
634 length up to 73 cm, rarely longer, and circumference of base 22 to 27 cm (M 24.5). Females invariably bear horns.

General body color rusty-cinnamon; light-colored spots on sides absent. Tress on chest and neck well developed and forms something of a beard on throat and base of lower jaw.

Found on right bank of the Amu-Darya and lower Pyandzha eastward to the Darvaza. Not known outside the USSR.



635 Fig. 216. Bukhara mountain sheep, *Ovis ammon bocharensis* Nasonov. Sketch by A.N. Komarov.

C. Group *cycloceros*—Turkmenian Sheep

4. Turkmenian sheep,[286] *O. a. cycloceros* Hutton, 1842 (syn. *arkal, arkar varenzovi*).

Larger in size than all the preceding races. Height at withers in males 92 to 95 cm; maximum skull length in males 257 to 297 mm (M 272) and in females 231 to 263 mm (M 249).

Facial part of skull elongated and constitutes, on the average, over 60% of maximum length of skull. External nares longer and broader than in preceding forms and nasals narrow. Profile of skull behind horns dips more steeply than in preceding forms.

Horns markedly larger and heavier. Maximum length up to 92 cm and circumference of base 24 to 30 cm (M 26). Horns homonymous (with a definite positive curvature); exceptionally horns bent in single or almost single plane (highly perverted). Outer rib well developed; frontal surface flat or slightly concave, and not tapered out ward or only poorly so; temporal surface flat; and transverse folds prominent and well projected. Females mostly with horns.

Color yellowish-rusty; light-colored spots on sides absent. Tress luxuriant, and light-colored beard present on throat and at base of lower jaw (for more details, see Fig. 212).

Found in uplands and elevations of extreme southern Turkmenia (Karabil', Chengurets mountains east of Kushka, Badkhiz, Gyaz'-Gyadyk), Kopet-Dag, Great Balkhan, rugged and elevated sites on the east coast of the Caspian Sea, Mangyshlak, and Ustyurt. Outside the USSR occurs in northeast Iran and Afghanistan.

The sheep of Mangyshlak are usually taxonomically separated from those inhabiting Kopet-Dag under the name *O. a. arcal* (for example, Tsalkin, 1951). Yet they differ from Kopet-Dag sheep essentially in the absence of animals with perverted horns and a more intense beard development. These features, also reported in a few animals from Mangyshlak, require confirmation and, moreover, are very insignificant. If such sheep do exist, then they merely represent individuals exhibiting extreme development of features of the form *cycloceros,* and thus there is no justification for isolating them as a separate race. No actual geographic isolation whatsoever has occurred between the two groups, at least not until very recently.

The inclusion of Turkmenian sheep in the form *cycloceros* described from southern Afghanistan (Kandahar) requires confirmation. Some authors combine sheep from southern Afghanistan with those of Baluchistan, separating them from Khorasan, Kopet-Dag, and Ustyurt sheep (Lydekker, 1913). This view is evidently justified. If so, Turkmenian sheep should be called *arcal* Eversmann or, if Mangyshlak (Ustyurt) sheep are excluded, *varenzovi* Satunin. Sheep of northern Afghanistan (Afghan Badkhiz), adjoining southern Turkmenia, should be placed in the Turkmenian form. (V.H.)

---

[286] Formerly this form was known as the Kopet-Dag sheep and more recently sometimes labeled Afghan sheep. This is an undesirable practice. Older workers (Pallas, 1811; Eversmann, 1850; and others) called the northern populations of the species from the eastern shore of the Caspian Sea, Mangyshlak, and Ustyurt ("*O. arcal*") "steppe sheep".

636 The foregoing form is unique in that unlike various other forms it has well-developed features transitional between eastern and western groups and combines the features of both (see various features depicted under "Description").

5. Kyzylkum sheep, *O. a. severtzovi* Nasonov, 1914.

Somewhat smaller in size than Turkmenian sheep (*O. a. cycloceros*). Maximum length of skull in males 260 to 270 mm (M 265).

Lacrimal depression poorly developed.

Horns homonymous and resemble those of Turkmenian sheep in flexure and size. Maximum length of horn 73 cm and circumference of base 23 to 26 cm (M 24).

General color darker, grayish-cinnamon or grayish-brown. Tress on neck and chest weakly developed, short, and does not reach base of head; beard absent.

Found on elevations in the Kyzylkum, especially Aktau and Nuratau (? Turkestan range). Not known outside the USSR.

In some features this form is intermediate between the moderate-sized *cycloceros* group and the large sized *polii* group, and links the two groups very well. The weak growth of the tress in this form is a feature of the latter group, while the structure of its skull and horns resembles that of the former. It inhabits a geographically intermediate territory between the areas of occurrence of the two primary groups, i.e., between the Ustyurt and Pamir-Alai systems (through Sultan-Uizdag east of the Amu-Darya delta, Aktau, and Nuratau) and to a lesser extent the Tien Shan. This race is apparently hybrid in origin.

D. Group *polii*—true arkhar sheep

6. Karatau sheep, *O. a. nigrimontana* Severtzov, 1873.

Much larger than Turkmenian (*cycloceros*) and Kyzylkum (*severtzovi*) forms. Maximum skull length in males 285 to 315 mm (M 303) and in females 258 to 274 mm (M 268).

Skull structure similar to that of Turkmenian form (*cycloceros*) but skull profile behind horns steeper. Occipital region projects little beyond line of rear edges of bony cores, facial part of skull higher and broader, prealveolar portion of upper jaw somewhat longer, and nares and nasal bones broader.

Horns large, homonymous, and up to 102 cm long; circumference of base 28.5 to 33.5 (M 31).

General color darker than that of Turkmenian form, brownish with a cinnamon or rusty tinge. Tress poorly developed; elongated (up to 11 cm) hair only present on chest and lower portion of neck.

Found in Karatau. Absent outside the USSR.

The features of the group to which *O. a. nigrimontana* belongs are expressed least sharply in this form. In skull structure it is distinctly intermediate between the *polii* group and the *cycloceros* group (forms *severtzovi* and *cycloceros*).

7. Tien Shan sheep, *O. a. karelini* Severtzov, 1873 (syn. *heinsii, nassonovi, melanopyga*).

Larger than the preceding forms, standing about 110 cm high at the withers. Skull length 305 to 335 cm (M 324).

Facial part of skull relatively longer, higher, and broader than in form *nigrimontana* and constitutes 60 to 63% of maximum length of skull. Nares longer and broader. Interpterygoid fossa broad and articular surfaces of occipital condyles very large. Skull behind horns projects little beyond line of rear edges of bony cores, and its upper profile steep.

Horns larger than in preceding form, length reaching 129 cm, and circumference of base 33 to 40 cm (M 36). Terminal portion of horns relatively weakly bent sideways, rising up almost parallel to
637 base. Outer ridge of horn somewhat more indistinct than in preceding forms and base of horn blunted.

General shade of body color lighter, brownish-yellow or brownish-cinnamon. Tress absent but hair on front of chest and base of neck slightly elongated (up to 10 cm).

Found in the Tien Shan south to the Narym and the Ferghana range inclusively, and west to the western extremity of the mountains, including Kirgiz (Aleksandrov), Talas, Ugam, Pskem, and Chatkal' ranges. To the east and southeast in the Kokshaal and Aksai, this form has apparently been replaced by another. The range in the north includes the Chu-Ili mountains. Absent outside the USSR.

8. Kazakhstan sheep, *O. a. collium* Severtzov, 1873 (syn. *sairensis, albula, obscura*).

In size of body, skull, and horns, this form is identical to the preceding one.

Ascending processes of premaxillae very long and extend posteriorly between the nasals and maxillae; ends of processes separated from lacrimals only by a small commissure formed by upper part of maxillae.

Outer ridge of horn even more faintly developed than in preceding form and temporal surface more convex.

General color usually a dark vivid brownish-cinnamon (light-colored animals also known).

Found in Kazakh *melkosopochnik* westward roughly to the meridian of Ulutau and Akmolinsk (to 67–70° E long.), in the east to the Irtysh, and in the south to the Saur, Tarbagatai, and the northern coast of [Lake] Balkhash. Outside the USSR associated with the Saur and Tarbagatai mountains in northwestern Dzhungaria [China].

This form is not readily distinguishable from Tien Shan *O. a. karelini*. Evidently only the coloration and the above craniological characters differentiate it and these, too, only after an inspection of a large number of animals. In all probability this form and the Tien Shan form are identical. (V.H.)

9. Pamir sheep, *O. a. polii* Blyth, 1840 (syn. *poli, typica, littledalei, humei*; incorrectly spelled by various authors *poli* or *poloi*).

Larger in size than the two preceding forms. Height at withers up to 120 cm. Maximum skull length in males 328 to 355 mm (M 341) and in females 283 to 305 mm (M 295).

Skull behind horns projects even less backward beyond line of rear edges of bony cores. Line of upper profile steeper. Interpterygoid fossa broader.

Horns larger than in all the forms described thus far. Length may reach 190 cm and circumference at base 35 to 40 cm (M 37). Terminal part of horns highly twisted outward.

Color dark grayish-reddish-brown, sometimes chocolate. Tress on neck and chest slightly larger than in other forms of this group and reaches 18 cm in length (see "Description").

Found in the Pamir, eastern extremity of the Alai range, Aksai Plateau and Chatyrkel' region, Kokshaal to Khan-Tengri in the north, and Dzhungar Alatau. Outside the USSR occurs in the Chinese sector of the Tien Shan and mountains adjoining the Pamirs.

The relation of this form to Tien Shan *karelini* with regard to taxonomy and geographic distribution is not very clear. This is particularly true in the region of the Kokshaal and in the Dzhungar Alatau. These two forms are very closely related (differences discernible only in large numbers) and their affinities call for a review. Evidently the forms *polii, karelini,* and *collium* should be combined into one. (V.H.)

E. Group *ammon*—Argali

10. Altai sheep, *O. a. ammon* Linnaeus, 1758 (syn. *argali, altaica, daurica, mongolica, ammon typica, przevalskii, asiaticus*).

Largest of all the races inhabiting the USSR as well as of all the various races that constitute the species. Height of males at withers 638 up to 125 cm and maximum skull length in males 345 to 385 mm (M 360) and in females 305 to 337 mm (M 318).

Skull structure very similar to Pamir race (*polii*), differing only in greater length of the anteronasal profile and greater width of skull in region of ears and brain case. Bony bases of horns massive and broad.

Horns very large and strong, with a much broader and massive basal portion than in Pamir form but not as long. Maximum horn length up to 125 cm and circumference of base 40 to 50 cm (M 44). Outer rib of horn usually weakly developed and may totally disappear in basal portion of horn. Temporal surface convex, especially at horn base.

Found in Altai, Tuva, and Trans-Baikaliya (now extinct). Outside the USSR found in northern Mongolia.

In addition to the above autochthonous forms, a member of the *musimon* group, i.e., mouflon, is also acclimatized in the USSR.

11. Mouflon, *O. a. musimon* Pallas, 1811. (For name of this form, see synonyms of species, pg. 881.)

One of the smallest races of this species. Height of males at withers about 75 cm. Maximum skull length in males 226 to 245 mm (M 233) and in females 210 to 222 mm (M 216).

Facial part of skull short (not more than 58% of maximum skull length). Occipital region projects strongly backward beyond line of posterior edges of bony cores. Upper profile of this section of skull gentle. Premaxillae short and usually do not reach nasals. Latter broad while nares short and narrow.

Horns absolutely and relatively small. Maximum length up to 75 cm, rarely greater. Circumference at base 20 to 23 cm (M 21.5). Curvature of horns highly variable. Perverted horn apparently a characteristic feature of this form but homonymous and even heteronymous horns (with a negative bend) are often seen. Outer ridge of horn not well developed or not visible. Frontal surface highly tapered laterally and transverse folds on surface of horn smaller. Females almost invariably without horns. Color of horns a dark cinnamon.[287]

General color of body dark cinnamon; sides of males with white spots which are highly variable in form and size.[288] Small tress of dark hair occurs on chest; does not reach base of head (see "Description").

---

[287] The only instance in the species as well as in the genus.

In the USSR mouflon have been acclimatized and live in the Crimean preserve (since 1913). Crimean mouflon are not wholly pure-blooded: ten Corsican mouflon and three with an admixture of blood of domestic sheep from Askaniya-Nova were introduced in this area (Dal', 1958); nevertheless, the animals are fairly typical.

The natural distribution of mouflon encompasses Corsica, Sardinia, and Tavolara [Island]. Outside the USSR acclimatized mouflon live in Holland, Luxembourg, France, Italy, Switzerland, Austria, Czechoslovakia, Hungary, Yugoslavia, Rumania, and Poland.

Numerous forms of sheep have been described from different areas of the geographic range of the species outside the USSR. The following are more often recognized: true mouflon, *O. a. musimon* Pall., 1811 (see above); Cyprus sheep, *O. a. ophion* Blyth, 1841—Cyprus; Asia Minor sheep, *O. a. anatolica* Valenc., 1856—southern regions of Asia Minor; Urmian sheep, *O. a. urmiana* Guenth., 1899—Koyun-Dagy Island in Lake Urmia; Isfahan sheep, *O. a.*
639 *isphaganica* Nas., 1910—western and southwestern Iran; Laristan sheep, *O. a. laristanica* Nas., 1909—southern Iran; Punjab sheep, *O. a. punjabensis* Lyd., 1913—Punjab and the Solon mountains; Baluchistan sheep, *O. a. blanfordi* Hume, 1877—eastern Baluchistan; and Elburz sheep, *O. a. orientalis* Gmel., 1774—Elburz. These forms belong to the western (mouflon) type of sheep.

The following forms of sheep from the argali group (*ammon*) are usually recognized from areas east of the Soviet Union; Yabarai sheep, *O. a. kozlovi* Nas., 1913—Yabarai mountains in the southern Gobi; eastern Tibet sheep, *O. a. jubata* Pet., 1876—mountains of Inner Mongolia and northwestern part of China proper, Alashan, Nan' Shan, and eastern part of the Kunlun; western Tibet sheep, *O. a. dalai-lamae* Przev., 1888—western Tibet from the Altyntagh, Tokus-Daban, and the Russian range on the north to the Przheval'skii range in the south; and Himalayan sheep, *O. a. hodgsoni* Blyth, 1841—Himalayas from Kashmir to Sikkim in the east.

The characteristic features of some of the races listed above have not been fully established and their independent status is dubious. In the west, the form *anatolica* is very close to *gmelini* and probably identical to it. Similarly the characteristics and affinities of the form *isphaganica* are not clearly known and very little is known about the form *laristanica* (to date there is only one specimen!). The forms *punjabensis* and *blanfordi* are apparently identical. Similarly the status of *orientalis* from the Elburz as an independent form is highly dubious. Evidently, it represents a hybrid population occurring in the zone of contact between the ranges of the *gmelini* and *cycloceros* groups. The independence of some forms of the *ammon* group inhabiting Central Asia is also dubious.

---

[288] Sometimes in winter individuals are seen with a very dark, almost black coloration and without white spots. In Slovakia where mouflon were acclimatized in 1880, this mutant form became predominant, displaced the normal form, and extended the range farther (into Hungary). This form is sometimes considered a special subspecies, *sinisella* Turecek, 1949.

A revision of geographic variation in the species based on extensive material is essential. There is no doubt that such a study would lead to some reduction in number of forms. Geographic variation of the species nevertheless remains quite high. (V.H.)

Biology

Population. In prerevolutionary Russia the stocks of mountain sheep in many parts of the range were greatly depleted and at places the animals were even totally exterminated. This was effected not only by uncontrolled hunting, but also by the displacement of wild sheep from excellent pastures by shepherds, the adverse effects of which have been described by N. Severtsov (1873, 1873a). In the course of the eighteenth, nineteenth, and first quarter of the twentieth century, sheep disappeared from Aragats (Trans-Caucasus), Kuba-Dag (near Krasnovodsk), between the mouths of the Syr Darya and Kuvan-Darya, from the northwest Altai (Tigerets and other mountain ranges), all of southeast Trans-Baikaliya (Onon-Cholon, Soktui, Chir, etc.) and many other localities (Tsalkin, 1948 and 1951).

With the exception of a few regions where conservation measures were effected soon after the October Revolution and the Civil War, in the rest of the range the population of mountain sheep in the USSR has continued to decrease even in recent decades. In the second quarter of the twentieth century sheep disappeared from the Little Balkhan range and the population decreased in the Trans-Caucasus, Kopet-Dag, Ustyurt, and Tien Shan mountain systems (for example in the Trans-Ili Alatau), at places in the Pamir, and in certain other regions of the country. In most cases this was assisted by the rapid colonization of regions by man, which had before been thinly populated (for example, the east shore of the Caspian Sea, Karakum, Kyzylkum, and Pri-Balkhash, etc.). The range thus split gradually into isolated pockets with sparse populations of sheep. In this process not only excessive hunting but also the appearance of large packs of wolves, epizootic diseases, severe winters, etc. often proved fatal. At present mountain sheep have been preserved in substantial numbers mainly in Pamir and Tien Shan, but no precise data about their numbers are available.

In one day Meklenburtsev (1948) counted, in the summer of 1937, 640 some 20 to 25 argali sheep in the Alichur valley (eastern Pamir) in an area (more correctly projections of slopes) of 1,500 to 2,500 hectares; this means roughly 12 animals per 1,000 hectares. There were about 300 sheep in the Bash-gumbaz valley and on adjoining slopes over an area of 25,000 to 30,000 hectares. In the Mergen-ul' region (central Kopet-Dag) some 480 sheep were counted on February 18, 1942 (Tsalkin, 1948). In subsequent years sheep in the central Kopet-Dag decreased progressively. In a territory of some tens of thousands of hectares in the Aksu-Dzhabaglin preserve (western Tien Shan), there were not more than 60 to 80 argali sheep in 1933 to 1935 (Shul'pin, 1948). In the summer of 1950, 670 animals were counted, and after the severe winter of 1951, 512. In later years the sheep population increased in the Kazakh *melkosopochnik* where at one time they were on the verge of total extinction. At present there are about 3,000 of these animals (A.A. Sludskii). A perceptible increase in the population of sheep has also occurred in the Crimean preserve, inhabited by Corsican mouflon with an admixture of blood of domestic sheep imported there from Askaniya-Nova in 1913. In 1941 the mouflon population in the preserve numbered about 500 animals, but during the war and subsequent occupation of Crimea the number decreased to 30 to 40 (Yanushko, 1955); by 1958 it had again risen to roughly 250. Some data are available about the population of sheep in the former Alma-Ata preserve region (Sokolov, 1939; and others), western Chink of Ustyurt (Bazhanov, 1945), and other regions. No other data are available on the population of mountain sheep.

A comparison of the herd index of mountain sheep in different years reveals that in many parts of the range the sheep population has decreased tenfold in the last 50 to 80 years. Obvious exceptions to this are mainly the Pamir and sparsely settled areas in the Tien Shan, where groups of 300 or more animals are encountered even now in the cold season in the Pamir and 100 or more in the Tien Shan according to Meklenburtsev (1948). Sheep are quite common in Badkhiz; in Gyaz'-Gyadyk herds of 200 to 300 animals were sighted in the 1940's (Heptner, 1956).

Habitat. Mountain sheep inhabit mainly open expanses with a slightly rugged relief: plateaus, gentle slopes of hills, ridged foothills, *melkosopochnik*, etc. They usually avoid sections with an intensely rugged, rocky topography and, in this respect, differ not only from mountain goats but also from snow sheep. In relatively large valleys sheep are rarely seen and then, too, only as stray animals during migrations. They are also absent in areas covered by fairly dense forest vegetation. They particularly inhabit pastures with low-grass or hill-steppe vegetation. They live under arid conditions in the Ustyurt, Bet-Pak-Dala, and other regions of Middle Asia. In the Badkhiz they live in a very severe desert with poor water sources (Heptner, 1956).

A wide range of vertical distribution is characteristic of mountain sheep in the USSR—from heights below sea level (Caspian coast) to 4,500 to 5,000 m.[289] Quite often different populations of one and the same subspecies, for example Tien Shan sheep (*O. a. karelini*), live in a mountain belt from several hundred to 4,000 m or even higher (Severtsov, 1873). Of the subspecies inhabiting the USSR, only Pamir sheep (*O. a. polii*) which live in the high drainages of the uplands of the Pamir and Tien Shan and do not descend below 3,000 to 3,500 m may be considered a high-altitude mountain form. On the whole, however, *O. ammon* is a euryzonal species (Tsalkin, 1951).

Although mountain sheep are attracted to open pastures with a commanding vista and smooth relief where they can save themselves from enemies by running away rapidly,[290] preference is often shown
641 for montane areas which provide cliffs or gorges, as well as gentle and comparatively broad pastures. When needed, sheep find at such places shade on hot days and protection from wind in winter, and sometimes even refuge from enemies. In search of shade, refuge, and during migrations, sheep are found on slopes covered with sparse juniper (Kopet-Dag and Khan-Tengri), pistachio (Badkhiz and lower Vakhsh), or even tall arboreal vegetation (Crimea); quite often sheep graze on these slopes or keep entirely to them (Badkhiz; Heptner, 1956).

Many regions in areas now inhabited by mountain sheep do not satisfy their biological requirements and the animals have been displaced by shepherds and hunters. Even N. Severtsov (1873) noted that the seasonal distribution of sheep in the eastern Tien Shan, in the Semitau and Arkalyk mountains, in the upper courses of the Chuya in the Altai, etc. depended greatly on the distribution of livestock in the mountain pastures and on periods of herding. According to Severtsov in some regions wild sheep were confined in winter to untrampled sections of summer livestock pasture and displaced in summer to wintering sites. Later, similar phenomena were observed in the Susamyrtau (Chernavin, 1916), eastern Pamir (Meklenburtsev, 1948), Kopet-Dag (Tsalkin, 1948), and other parts of the range. In the mountains of the Syr Darya Karatau and in the Nuratau range sheep, while attempting to save themselves from innumerable wolves and hunters, were compelled to live on steep, extremely rocky slopes and along gorges, i.e., in habitats quite unusual for them (Severtsov, 1873; Meklenburtsev, 1936; and others).

---

[289] In the Himalayas sheep are found at even greater heights. The statement by Meklenburtsev (1948) that Pamir sheep are confined to summer pastures at heights of 4,500 to 5,500 m is not correct; pastures are absent above 5,000 m in the Pamir and the lower boundary of the nival belt runs at a height of 4,700 to 5,400 m (Egorov, 1955).

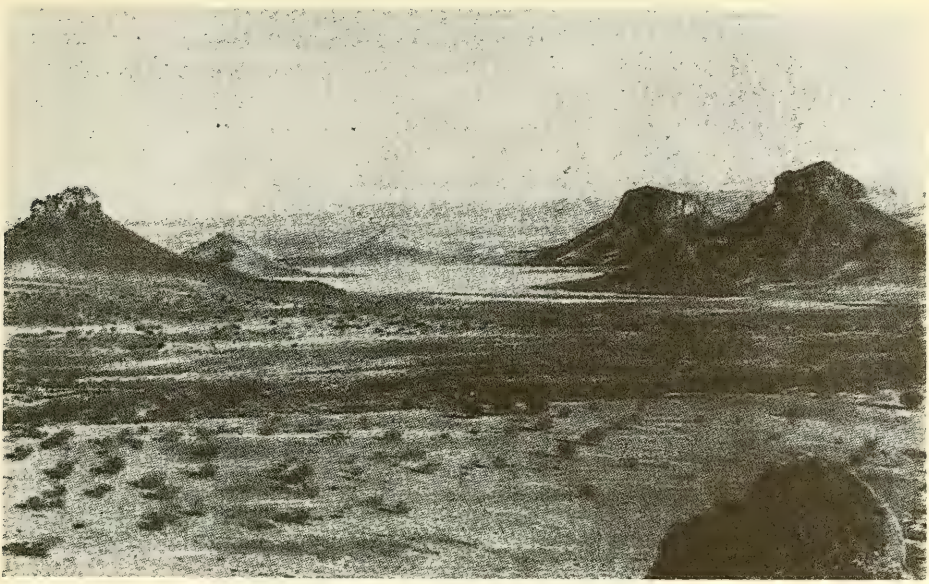
[290] On steep and rocky slopes sheep are quite inferior to goats in speed and agility.

The conditions of existence of sheep in the semidesert and desert regions of the Trans-Caspian (Ustyurt, Mangyshlak, Lake Er-oilan in the Badkhiz, and others), Kyzylkum, Bet-Pak-Dala, and Kazakh *melkosopochnik* are very typical. Sheep often live in these regions along low remnant hills rising to only 100 to 200 m above the surrounding sandy areas and solonetzes; from there they regularly visit gorges and ravines where vegetation withstands withering 642 longer and snow and rain water collect at the bottom in depressions ("potholes") (Bazhanov, 1945; Beloslyudov, 1948; Tsalkin, 1948; Afanas'ev et al., 1953; Heptner, 1956). On the coast of Kara-Bogaz-Gol-Bay sheep were found in immediate proximity to the Caspian Sea in the early 1930's (Tsalkin, 1951).

In the snowfree period of the year adult male sheep usually prefer more elevated and less accessible montane areas than do females and juveniles.

In mountainous regions, with the approach of winter, sheep usually descend to lower levels, to regions with relatively abundant snow. For example, in the Khan-Tengri, Trans-Ili, and Dzhungar Alatau the range of vertical migrations varies from 1,500 to 2,000 m (Nasimovich, 1955).

Food. On the whole no less than 180 plant species are known to be eaten by mountain sheep within the USSR, but a thorough study of their food in different regions has not been made except in the Crimea. Thus, while the intake by sheep of not less than 132 plant species has been established for the Crimean preserve (Yanushko, 1955), no more than 20 to 25 species have been recorded in each of the mountain regions of the Kopet-Dag, Pamir, and Trans-Ili Alatau, and some 10 species in the Ustyurt. Information is generally more fragmentary for the remaining regions. Over much of the range grasses are of maximum importance in the diet of sheep (some species of the genus *Festuca*, especially sheep's fescue *F. sulcata*, wheatgrass *Agropyrum*, meadow grass *Poa*, feather grass, etc.), several species of forbs, sedges in high montane habitats (of great



641 Fig. 217. Basin of Lake Er-oilan-duz in the Badkhiz (southern Turkmenia). Remnant hills and precipices of the chink (in background) serve as habitats of argali sheep. June, 1948 (see also Fig. 243). Photograph by V.G. Heptner.

importance in the Pamir), and halophytes (*Anabasis* and *Salsola*) in semidesert regions. Sagebrush is consumed in arid regions where the composition of food is very limited but utilized only in winter in other parts of the range. Sheep also consume onion. In the Badkhiz the main food year-round is green or dry meadow grass (*Poa bulbosa*) and sedge (*Carex physodes*) (V.G. Heptner).

In the central Kopet-Dag the main summer food plants are wheatgrass, astragalus, feather grass, and fescue, which are abundant in mountain steppes and constitute the main mass of herbage; sheep consume them well both in green and dry states (Tsalkin, 1948). In the Trans-Ili Alatau sheep consume in early June mainly bear's reed [angelica] *Archangelica songorica, Calianthemum,* sedge *Carex tristis,* and two species of onions of the genus *Allium,* and later bistort *Polygonum* (four species), geranium, and others (Sokolov, 1939). In the Dzhungar Alatau the stomachs of sheep caught in summer contained mainly *Spirea hipericifolia, Zygophyllum,* saltwort *Anabasis,* sheep's fescue, feather grass, and *Atraphaxis.* Feather grass and *Atraphaxis* predominated in the stomachs in spring, but the onion *A. galantum* constituted up to 90% of stomach contents in autumn (Antipin, 1941).

642 Fig. 218. Clay "cliffs" and rocks in the Kyzyl-Dzhar gorge ("arkhar cliff") in the Badkhiz (southern Turkmenia) providing shaded shelter for argali sheep during summer heat. June, 1948. Photograph by V.G. Heptner.

643 In the eastern Pamir in summer these sheep often consume sedge of the genus *Carex, Kobresia,* meadow grass, sheep's fescue, feather grass, wild barley *Hordeum,* and *Roegneria,* and in spring and early summer *Primula nivalis, Delphinium,* and others (Meklenburtsev, 1948). In the stomachs of steppe sheep caught in the Ustyurt remnants of saltwort *Anabasis turgaica* predominated; other plants (common reed *Phragmites communis,* caragana, and others) were present in small quantities (Bazhanov, 1945).

Apart from spirea and caragana the Middle Asian subspecies of sheep consume from other shrubs and trees in summer the leaves and shoots, and fruits of pistachio as well as the hard shell (Gromov, 1937; Heptner, 1956). On Baga-Bogdo mountain (Ubur-Khangai aimak in Mongolia) sheep consume a number of other plants, including the branches and leaves of winterfat *Eurotia,* almond, caragana, elm, cotoneaster, willow, and aspen (Dordzhiin, 1958).

Dead herbaceous material forms the main constituent of the winter diet of sheep; at places branches of shrubs are of no mean importance. In the eastern Pamir, as long as the snow cover is not deep, sheep consume sedges, often eating them clean (uprooting grass is generally very characterisitic of sheep). As soon as the low sedge is covered by snow, the animals turn to taller plants such as wild barley, *Roegneria,* meadow grass, mountain fescue, and feather grass. Toward the end of winter, when these too are covered by snow, sheep feed mostly on portions of sagebrush and winterfat *E. ceratoides* projecting above the snow (Meklenburtsev, 1948). In winter sheep graze mainly on windblown sections; they very rarely resort to digging up food from under the snow with their hooves, and that only when the snow cover is soft and not more than 15 to 20 cm high. Lichens and moss are consumed very rarely (Severtsov, 1873; Yanushko, 1955) and hay only occasionally (Antipin, 1941). When other food plants are scarce in winter, sheep take to juniper needles (Kopet-Dag) and even saxaul shoots *Arthrophytum persicum* and tamarind (Dzhungar Alatau).

The food of Crimean sheep is extremely typical. They often enter the forest and quite frequently nibble at the leaves, shoots, and twigs of trees and shrubs, sometimes in significant quantities, even in summer. For example, the stomach of a sheep caught on August 12, 1950 contained 70% (by weight) leaves of hornbeam and oak. Of the 118 plant species consumed by Crimean sheep in summer, 6 are herbaceous and 9 shrubby. The main constituent nevertheless is herbaceous vegetation, especially geranium *Geranium sanguineum,* orchard grass *Dactylis glomerata,* and wall germander *Teucrium chamaedrus,* which comprise 22% of intake. The main winter food of Crimean sheep consists, in addition to grasses (orchard grass and wheatgrass) and sedges (*Carex digitata*), of hornbeam, beech, oak, jasmine, maple, and others. Among deciduous species sheep consume in winter the twigs, shoots, buds, and dry leaves of oak and the needles of pine and juniper; sheep never eat bark. In spring Crimean sheep feed on the shoots of *Primula,* asphodeline, snowdrop, squill, peonies, and other plants (Yanushko, 1955).

In the Badkhiz the stomachs of mountain sheep contained beetles, phalangids and scorpions; these were also found in the stomachs of domestic sheep (Gromov, 1937). Sheep can go without water for a long time (Ognev and Heptner, 1929; Sokolov, 1939; and others); they may lap extremely saline water and sometimes even muddy oozes (Flerov and Gromov, 1935; Heptner, 1956; and others). In the eastern Pamir where saline outcrops in the form of blooms cover extensive sections, sheep lick them while nibbling grass (Egorov, 1955). In other parts of the range, they go, or did in the past, to dry and wet salt licks (Crimea, Syr Darya Karatau, Trans-Ili Alatau, Altai, and others).

Home range. For much of the year, except for the time of shifting between summer and winter biotopes, which occurs in autumn and spring, sheep spend a fairly settled way of life. In the mountains of the Aksu-Dzhabaglin preserve the daily movements of sheep in summer are from 3.0 to 5.0 km; in winter the animals are more settled and move within a narrow range (Shul'pin, 1948). A reduction in home range of a herd is observed in winter in most regions 644 where winter is relatively snowy and summer not very arid. For example, in the Badkhiz, where winters are snowy and summers arid, leading to the early desiccation of vegetation, the animals are compelled to spend much of the warm season near a few water sources and better-preserved pastures. In autumn, with the onset of growth of ephemerals, the size of sheep habitats on the other hand enlarges (Heptner, 1956).

Compared with mountain goats, sheep require much more extensive pastures (Severtsov, 1873). However, in many mountain ranges where sheep have been extensively displaced by shepherds or persecuted by hunters, they are compelled to confine themselves throughout the year close to cliffs in extremely limited territories.

Daily activity and behavior. In summer, especially if the weather is warm, sheep are most active in the early morning and twilight hours. Most animals graze from 7.00 to 8.00 a.m. and subsequently rest; only a few lone animals are found in pastures after 9.00 to 10.00 a.m. Some recommence grazing from 3.00 to 4.00 p.m., but if the heat is great grazing resumes only at 5.00 or 6.00 p.m. Grazing, apparently with intervals, extends even into the nocturnal hours (Flerov and Gromov, 1935; Antipin, 1947; Yanushko, 1955; Heptner, 1956). Water holes and salt licks are visited mainly in the evening or at night, but sometimes in the morning.

Depending on topographic features, elevation of locale, availability of protective sites, enemies, density of blood-sucking insects, atmospheric temperature, and other conditions, sheep make beds in almost the same regions where they graze, or else move up or down the slope, sometimes covering 1.0 or 2.0 km for this purpose. In summer in the high-montane parts of the Pamir and Tien Shan many sheep rest on open slopes, often on steep rubbly talus and sometimes on snow. In the eastern part of the Altai and in the Sayans sheep shelter during the day under cliffs, on rock streams, near montane saddles, and in cirques by small lakes.

In regions with a warm dry climate (Kopet-Dag, Badkhiz, moun-

tains along the lower Vakhsh, etc.) sheep in summer retreat to beds in gorges where there are cliffs or select sites where shrubs and trees provide shade. In the hills along the lower Vakhsh, Tadzhikistan sheep (*O. a. bocharensis*) rest under cliffs or at the base of pistachio trees, digging pits to a depth of 1.5 m with their hooves (Flerov and
645 Gromov, 1935). Sheep also like to rest in the shade of pistachio trees in Gyaz'-Gyadyk (Badkhiz). On slopes, under tree trunks, these animals dig "little balconies". In the Er-oilan-duz basin (Badkhiz) ledges on precipitous slopes of gorges serve as beds. The animals inadvertently broaden these ledges since their clay walls gradually crumble under the impact of horns, etc. Sheep change their beds in accordance with shifts in shade (Heptner, 1956).

In July and August Crimean sheep make beds in the forest, sometimes hiding in wind-fallen woods [blow-downs]. During the day solitary animals, often no more than 15% of the entire population, remain in open parts of the mountains (Yanushko, 1955). Sheep use the same beds with great regularity, particularly at places in which shade is scarce.

In overcast weather the rhythm of daily activity loses its regularity; sheep usually do not graze in heavy rain or during cold or windy weather. Instead they move to leeward slopes, into ravines, etc. In

644 Fig. 219. Trail of argali sheep in powdery solonchak by a water hole. Wild ass trails intersect pathway. Kyzyl-Dzhar gorge in Badkhiz (southern Turkmenia). Photograph by V.G. Heptner.

regions where they are frequently threatened by hunters and shepherds the daily rhythm may also be interrupted. During the day they are compelled to stay on high cliffs where vegetation is meager, descending at night to pastures already grazed by cattle (Chernavin, 1916).

Daily migrations often occur along the same paths so that well-beaten trails are formed. In the Tien Shan mountains sheep sometimes use for travel the channels of spring freshets and mud slides (Antipin, 1947). During migrations sheep move in single file, quietly; while grazing they scatter; when frightened, they run in a dense herd (Meklenburtsev, 1948).

645 Fig. 220. Trail of argali sheep at the bottom of Kyzyl-Dzhar gorge in Badkhiz (southern Turkmenia). June, 1948. Photograph by V.G. Heptner.

In winter sheep graze mainly during daylight hours. Hours of rest and grazing are not the same in different herds but the period of rest in the bed, compared with summer, is nevertheless greatly reduced. During intense snowfall, wind, and cold sheep are confined to leeward slopes, troughs, protective rocks, or even forests (Crimea). Sometimes they dig pits in the snow with their hooves and rest in them, indifferent to being covered with snow (Pamir).

Depending on the animal's condition, age, sex, and season of the year, the weight load on the hooves of Crimean sheep varies from 280 to 818 g per cm^2 of contact area, averaging close to 660 g (Nasimovich, 1955; Yanushko, 1955); the latter value is close to the weight 646 load on the hooves of Altai argali also (Dul'keit, 1956). Hence sheep, especially of diminutive races, experience serious difficulties in moving on snow. For example, Crimean mouflon negotiate with relative ease snow not more than 20 to 25 cm deep; at a depth of 35 to 40 cm they break the snow with their stomachs and move their legs with great difficulty (Yanushko, 1955; and others). When the snow cover is even deeper, they advance in hops but cannot run for long. As mentioned earlier, sheep are minimally capable of digging out snow with their hooves.

Sheep possess well-developed sense organs. According to most observers they rely first and foremost on their sense of smell, followed by sight or audition (opinions about the latter are contradictory).

Large mixed herds of sheep consisting of 100 or more animals have been observed mainly in autumn or at the end of winter, continuing up to spring. Thereafter large herds dissolve since females before giving birth leave the herd (see "Reproduction"). Large congregations have been sighted immediately after a severe snowfall; such groups are not permanent and split readily into much smaller units (Meklenburtsev, 1948; and others). On rare occasions large herds of 300 to 400 animals have been sighted even in summer. Apparently these were chance congregations formed partly because of migration from burnt-over areas in the steppes (Badkhiz; Heptner, 1956).

Many other animals use the trails made by wild sheep (Flerov and Gromov, 1935). It has even been said that argali sheep are alert to the alarm calls of marmots (Sokolov, 1939) and the distress cries of other animals. In the Crimea the first leader of a herd of mouflon set free from a pen in 1917 was purportedly a female Dagestan tur (Shereshevskii, 1931).

When the population of wild sheep is high, as in the case of other herding ungulates, these animals can alter the microrelief and pasture composition. In the past in the eastern Pamir argali sheep grazed all the vegetation and thus greatly exhausted the pasture by promoting weathering of soil in scattered pockets; later, shifting sands formed in the region (Stanyukovich, 1950).

Seaonal migrations and transgressions. In most regions wild sheep are characterized by more extensive seasonal migrations than typical mountain ungulates such as goats, tur, and chamois. Being fond of relatively gentle slopes, mountain sheep are very selective about suitable places for living. This often compels them, when vegetation becomes parched or with the approach of winter, to migrate tens of kilometers. Seasonal migrations involve great distances (or did so in the not so distant past) in the Trans-Caucasus, Turkmen-Khorasan mountains (Badkhiz), some regions of the eastern Pamir, and also the Talas, Trans-Ili, and Dzhungar Alatau. In the Trans-Caucasus while migrating to winter sites (southward across the USSR border into Iran), sheep in some years covered a route exceeding 100 kilometers (Sarkisov, 1944; Nasimovich, 1955), in the eastern Pamir up to 50 to 70 km,[291] and in the region of Aksu-Dzhabaglin sanctuary up to 40 to 70 km (Shaposhnikov, 1956). The immediate reasons for such extensive migrations of sheep in these regions are diverse and have not yet been adequately studied; the nature of the configuration of mountains, the degree of winter snowiness and summer aridity, state of pasture in different seasons, magnitude of seasonal livestock-rearing, persecution by hunters, etc., play an important role.

In some regions, more often in foothills, relict mountains, and semi-deserts and deserts, part of the population remains in the same area throughout the year.

647 The wintering sites of sheep are usually located on the southern slopes of mountains and on windblown sections almost devoid of snow. The importance of the latter is particularly great in montane regions with a frosty [cold] winter (Pamir, central Tien Shan, Altai). Quite often sheep congregate in large herds in wintering sites on the leeward slopes of "mountain screens," which intercept part of the precipitation (Sinabdag range in Crimean preserve, Syr Darya Karatau, and eastern extremity of Trans-Ili Alatau) (Nasimovich, 1955).

The vertical range of seasonal migrations in high-montane regions with abundant snow may extend up to 1,500 to 2,000 m (Khan-Tengri montane complex, Trans-Ili, and Dzhungar Alatau). In mountains where the snow is less (eastern Pamir, highland drainages in the Narym River basin) sheep remain year-round at a great height, descending only several hundred meters in winter. In some regions, depending on the topographic features and human interference, sheep are confined in winter not to lower levels but to levels higher than in summer; such a phenomenon has been reported for the Tersk Alatau (Rumyantsev et al., 1935), Altai (Severtsov, 1873; Nikol'skii, 1883), and Mongolia (Dordzhiin, 1958).

---

[291] Extensive seasonal migrations of sheep in the Pamir have been reported by Egorov (1955). Meklenburtsev's data (1948) are apparently inaccurate; he denies migrations among argali sheep in the Pamir.

Distances covered during seasonal migrations and their vertical range often vary from year to year, depending on the aridity of summer (Sokolov, 1939) and the difficulties encountered by the animals in different winters (Sarkisov, 1944; and others). In the winter of 1948/49 sheep were seen during continuous snow in the environs of Kyzyl-Orda; three argali sheep were found in Borovoe preserve (Kokchetav district), which had covered a distance of not less than 500 km, and which remained in that region until 1951. In the winter following the drought of 1951, mass migrations of argali sheep occurred in Kazakhstan northward from the main range (Sludskii, 1954 and 1956). Extensive migrations of sheep in severe winters, and also in the following spring, have been observed in Dauria (Radde, 1861).

Migrations of sheep to wintering sites occur at different times in different parts of the range (from September through January), depending on the snow cover regime of different montane regions, periods of livestock transhumance, and so on. A mass migration of sheep commences quite often immediately after a heavy snowfall in the mountains (Nasimovich, 1955). The migratory periods of sheep vary greatly from year to year. For example, in the Crimea in the 1920's they occurred most often at the end of November through early December, but in 1927 were observed in October, and in 1926 only from the middle of December up to mid-January (Shereshevskii, 1931).

Return to the summer habitat occurs from the end of March to early April through June; females with young remain for the longest period in the lower parts of mountains (sometimes until July).

During migrations sheep, where possible, keep to their typical habitats; in the montane forest zone to open areas, short-grass meadows, comparatively gentle slopes, etc The route of seasonal migrations is highly constant; sheep generally negotiate rivers at fixed points. During migrations the animals move in large herds (Sarkisov, 1944; Nasimovich, 1955; F.D. Shaposhnikov, 1956; and others). In Mongolia, during migrations, sheep cross desert valleys 10 to 15 km wide where only scanty saxaul grow (Bannikov, 1954).

Instances are known of occasional sheep migrations triggered by steppe fires (Heptner, 1956).

Reproduction. The period of estrus differs in wild sheep in different parts of the range (from mid-October to mid-January) and also varies greatly in different years; estrus continues for 3 weeks to 1.0–1.5 months; young females are the last to come into heat. In the mountains of western, northern, and eastern Tien Shan estrus commences mostly from the latter half of October through mid-November, but was observed only from November 10–12 during 1949 to 1951 in Aksu-Dzhabaglin preserve (*Records of Nature in Aksu-Dzhabaglin Preserve*); i.e. later than the reported period. The latter half of November is the peak rutting period in the central Kopet-Dag; in this region it terminates toward mid-December (Tsalkin, 1948). Roughly similar periods (commencement of estrus from around November 20) have been recorded in Armenia (Sarkosov, 1944). Late estrus, recorded in the eastern Pamir, i.e., December and 648 the first half of January (Meklenburtsev, 1948), accords with the climatic conditions of that montane region. Spring there is severe and cold and hence early lambing females have little chance of saving their young. Rut in sheep in the high mountains of the central Tien Shan occurs only slightly earlier (December)*.

Information about the commencement of rut in mouflon in Crimean preserve is extremely contradictory. Here, various observers have reported periods ranging from October 20 through January, and even early February (Shereshevskii, 1931). Sheep were observed in the Crimea over several years and it may be stated that these references largely reflect the factual situation, i.e., wide variations in periods of rut in different years. It is possible that this is due to the formation of local mouflon populations with some admixture of the blood of domestic sheep. At present, rut in the majority of Crimean mouflon occurs most often in November (Yanushko, 1955).

Adult males and females, living separately in summer, form mixed herds even before the commencement of rut, i.e., in August or early September. With the onset of rut, most herds split into small groups containing one, two, or three adult males, several females of different ages, and juveniles including yearling males. True "harems" are not always formed therefore. The number of females in a group varies, depending on the total population and its sex ratio. In the eastern Pamir 8 to 25, more often 15, females have been counted in a harem (Meklenburtsev, 1948); in other regions their number is usually significantly lower, 5 to 10. Combats occur among adult males but result in no physical injuries as in some other ungulates, and only rarely the death of either rival[292] (Shereshevskii, 1931; Meklenburtsev, 1948; Tsalkin, 1948; and others). Adult males usually do not chase away juvenile males present in the herd.

---

*Contradictory in Russian original—Sci. Ed.

Spermatogenesis commences much before mating (a month or more). In one instance mature spermatozoa were found in a wild sheep killed in the Narym watershed region on May 9 (Rumyantsev et al., 1935).

Only some animals, and that not in all races, become sexually mature in their second year. In the highland drainages of the Narym where reproduction of wild sheep was studied using more advanced methods than employed in other regions, it was established that sexually mature males were aged not less than 2.5 years (Rumyantsev et al., 1935). All the gestating females caught in eastern Pamir were also not less than 2.5 years old (Meklenburtsev, 1948). In Kazakhstan (Antipin, 1941) males become sexually mature in their third year and some females even in their second. In the Crimean preserve only some females mature in their second year (Yanushko, 1955) and come into heat only in their third. Males four or five years do not mate since they cannot compete with older, more powerful males. All this renders difficult an accurate assessment of the periods of sexual maturity in these animals. Even among adults some females remain barren for various reasons. In some regions of Kazakhstan barren females constitute one-third of all female wild sheep older than 1.5 years (Antipin, 1947). The percentage of barren females increases after severe winters (*Records of Nature in Aksu-Dzhabaglin Preserve*).

Gestation lasts about five months or slightly more (but not six months as sometimes reported). In conformity with differences in periods of rut in different regions and years, periods of parturition also vary; lambing occurs from the end of March to mid-June.[293]

In Crimea in some years several females have lambed from March 25; in normal years, however, lambing occurs mainly in the latter half of April, sometimes right up to early May (Yanushko, 1955; and
649 others). Early parturition (in April) has been observed in the Talas, Trans-Ili, and Dzhungar Alatau (Sokolov, 1939; Antipin, 1941; Abduldabekov, 1948). In the Aksu-Dzhabaglin preserve from 1949 to

---

[292] Contradictory references (Severtsov, 1873; Sarkisov, 1944; Dordzhiin, 1958) have not been supported by direct observations.

[293] The statement by Antipin (1947) that parturition occurs in the Syr-Darya Karatau mountains from the latter half of February and ceases at the end of March is highly dubious.

1951 young lambs were sighted from April 12 to 29. According to Antipin (1941) sheep lamb mainly in early May in the northern parts of Asia (Kazakh *melkosopochnik,* Tarbagatai, and Altai). The last to lamb are sheep of the eastern Pamir (not before early June; Meklenburtsev, 1948) and central Tien Shan[294] (in the Tersk Alatau from the end of May but mainly in June; Egorov, 1955).

Usually one or two, more often one, and very rarely even three lambs are seen with a single female. Quite possibly the third lamb could be from a different mother. The first parturition generally produces a single lamb. In the Tien Shan mountains, of 66 females with lambs, 43 had one each (65%), 22 had twins (33%), and one had triplets (Antipin, 1947). In the Crimean preserve 92 female mouflon with young were sighted in spring and early summer from 1947 to 1950; of these only 11 (12%) had twins and the rest one lamb each (P.A. Yanushko). In the same region 228 female mouflon sighted from May to July had a total of 264 lambs among them, or an average of 1.15 lambs per female (Yanushko, 1955). It has been stated that more often two and not one lamb are usually borne in the Karatau (lower Vakhsh) and Armenia (Flerov and Gromov, 1935; Sarkisov, 1944); these data are evidently incorrect.

Before parturition the females separate from the herd. Parturition occurs in sheltered sites (often among rocks, by bushes, etc.), frequently in proximity to places where sheep winter. A few weeks after giving birth females and their young rejoin other females; immature males also join these herds.

Growth, development and molt. The great variation in size of adult wild sheep of different subspecies suggests that this difference is discernible even in newborns, becoming more pronounced with age. For example, one lamb (male) of the Turkmenian sheep, *O. a. cycloceros* (Kopet-Dag), at the age of a few days weighed 2.8 kg, while two two-day-old lambs of the Tien Shan sheep, *O. a. karelini* (highland drainages of the Narym region), weighed 4.44 kg (female) and 4.58 kg (male). At the age of six days the weight of Tien Shan lambs was 5.22 kg (female) and 6.0 kg (male). Such a weight or slightly more (to 6.0–7.5 kg) in lambs of Turkmenian sheep has been recorded only at the age of 1.0 to 1.5 months (Rumyantsev et al., 1935; Tsalkin, 1948). A lamb (female) of the Crimean mouflon four to five days old weighed 1.6 kg (Yanushko, 1955).

For the first few days after birth lambs are helpless and usually remain concealed in the grass. The female invariably grazes close by; suckling mainly occurs in the morning and evening. Roughly from the fourth day the lamb begins to accompany its mother. Feeding on grass commences at the age of one month (Shereshevskii, 1931), but lactation continues up to the end of summer or early autumn and even longer in some cases. In the Pamir two females with milk were caught on January 20 and February 2. Both were pregnant and had grown lambs with them (Meklenburtsev, 1948). The chemical composition of the milk of wild sheep is similar to that of domestic sheep (Antipin, 1947).

---

[294] In the highland drainages of the Narym region in 1934 lambing occurred even from the end of April (Rumyantsev et al., 1935).

Some juveniles begin to live independently in the autumn, but after the termination of rut many rejoin their mothers and remain with them until the birth of new lambs or even until the following autumn.

Female sheep attain maximum weight by their third year but males only by their seventh; thereafter weight increase is insignificant and mainly through fat deposition (Tsalkin, 1951). The most intense growth and weight increments occur in the first year. Crimean mouflon (males) weigh 10 kg by three months, 17 kg by eight months, and 24 kg by two years (in all cases only a single weighing was done); the mean weight of mature males was 33.6 kg (17 to 52 650 kg) and of females 26.8 kg (17.8 to 36.0 kg) (Yanushko, 1955). Male Turkmenian sheep (Kopet-Dag) at the age of nine months (February) weigh 20 to 22 kg, two-year-olds 34 kg, three-year-olds 38 to 46 kg, four-year-olds 48 to 58 kg, and other animals 85 to 96 kg. Females at the age of nine months weigh 18.5 to 20.0 kg and those older than two years up to 46 kg (maximum 56 kg). The mean weight of mature females is 36 kg and of males 63 kg (up to 75% heavier) (Tsalkin, 1951). Tien Shan male sheep (Narym) at the age of one year weigh 30.5 kg and at 3.5 to 4.5 years 101.0 to 110.5 kg; some sheep may weigh up to 180 kg (Denisov, 1935; Rumyantsev et al., 1935) or even slightly more—200 kg.[295] Thus sheep continue to grow even after attaining sexual maturity; the weight increase over the life span in males of some races is roughly 40-fold. Sexual dimorphism in size becomes increasingly perceptible from the second year; males are much larger.

The cheek teeth of sheep begin to appear in the first year of life. In the third year they have fully cut through (except for the underdeveloped sixth), and the premolars are ground down and shed in the fourth year. Dentition is fully developed by the fifth or sixth year (Antipin, 1947).

---

[295] Severtsov's (1873) statement that the weight of argali sheep may reach 18 poods (288 kg) is evidently unreliable.

Horns begin to grow soon after birth and continue to do so throughout the animal's life. There is apparently no juvenile shedding of horns among sheep. In all sheep the intensity of horn growth increases in the first two years (but in large races horn growth in the first year is relatively poor) and later slows down.

In races with large horns the curve of cessation of horn growth is very gradual.

The growth of horns lengthwise and in circumference is particularly intense for three to five years (Tsalkin, 1948 and 1951). In females the horns are considerably smaller; hornless females are also seen from time to time. The mane (tress on lower part of neck and chest), develops in males of some races of sheep only at the time of their second or third winter coat; it reaches maximum development only in fully adult animals (Tsalkin, 1951). Among Crimean mouflon the young are mostly light rusty in color, gradually darkening until at the age of three to four months their coloration approaches that of females; lateral spots are seen only in over-wintered animals (Shereshevskii, 1931).

The coarse guard hair with its air-filled core plays a special role in thermal insulation, rather than the underfur. Molt occurs only once a year, in spring; summer hair is not shed but remains until winter in the form of intermediate hair (Egorov, 1955). Depending on climatic conditions, molt occurs from the end of March to the first half of April (Crimea, Armenia, Kopet-Dag, western Tien Shan, etc.) or only from May (Pamir), and ends at the beginning of June to the end of July respectively. In the Pamir sheep with patches of winter wool on the back can be seen even early in August (Egorov, 1955), but in the Crimea usually until not later than the last few days of May (Yanushko, 1955). Juveniles, barren females, and males are the first to molt; females which have lambed are the last to molt, with a lag of 20 to 25 days (Antipin, 1947; Tsalkin, 1948; and others). The commencement of molt varies from year to year; for example, in the Aksu-Dzhabaglin preserve molt commenced in different years (1949 to 1951) from March 28 through April 10 (*Records of Nature in Aksu-Dzhabaglin Preserve*). During molt sheep are very sensitive to cold, confine themselves to well-insolated slopes, and try to protect themselves from rain.

The winter coat starts growing from the end of summer to early autumn. Crimean mouflon sport a winter coat toward the end of October to early November and Kopet-dag mouflon from October, before the commencement of rut. Males are seen in winter coat earlier than females.

The maximum life span of these sheep is 12 to 13 years (Tsalkin, 1951).

Enemies, diseases, parasites, mortality, competitors, and population dynamics. The wolf is the main enemy of wild sheep in most of their range. In trying to save themselves from wolves sheep usually run for open sections with a more or less even relief where they can 651 attain maximum speed (Ognev and Heptner, 1929; Denisov, 1935; Egorov, 1955); occasionally, however, they seek refuge among cliffs. According to Zverev (1948) juveniles of both sexes and adult females of argali sheep can reach 60 km an hour[296] and much heavier adult males with immense horns not more than 50 km an hour. The speed of wolf is about 45 km an hour. As a result of this speed ratio adult males are killed more often than females, especially in snowy winters. Furthermore adult males are often highly emaciated after the rut and thus tire quickly (Kolosov, 1939; Tsalkin, 1951; Sludskii, 1956). This feature is evidently most characteristic of large races of sheep, among which sexual dimorphism in body size and horn size is strongly manifested.

The magnitude of the predatory activity of wolves can be judged from the fact that about 20% of male argali sheep (of the animals counted; Egorov, 1955) were killed by wolves in some regions of the western Pamir in the severely snowy winter of 1950. Among these males sheep six years and older suffered the highest casualties. In taking a census of sheep in the western Pamir the age of over 200 males was determined with an accuracy of about one year. Thus 14% were two to three years old, 40%—four to five years old, 26%—six to seven years old, 17%—eight to nine years old, and 3.0%—older than nine years. The male sheep (61 animals) killed by wolves in this region were aged as follows: 6.6%—two to three years old, 21.3%—four to five years old, 39.3%—six to seven years old, 27.9%—eight to nine years old, and 4.9%—older than nine years. Thus, less than 10% of the population aged two to three years were killed by wolves, 12% of the four- to five-year-olds, 30% of the six- to seven-year-olds, and 30% of those over seven years of age (Egorov, 1955).

In a few regions where snow leopards are quite common (for example, Aksu-Dzhabaglin preserve), the damage caused by them to the sheep population can be dramatic. Leopards occur in Turkmenia mainly in regions where wild sheep are common (Heptner, 1956), but for the Soviet Union as a whole this predator, like the snow leopard, cannot exert a significant influence on the population of sheep. Cheetah, lynx, and even more so wolverine, seldom attack sheep (Altai, Sayans). These species are generally few in number in the habitats of sheep and, moreover, are specialized for hunting other quarry. Bear, spotted cats [*Felis libyca?*] (Morits, 1931), and some other predators might pose a danger only for young lambs. Sheep are threatened by the red wolf [dhole] only at places where these predators are common, i.e., outside the Soviet Union. In the Crimea when the population of foxes is high, they sometimes even attack adult female sheep (Rukhlyadev, 1939 and 1948; and others). In other regions only lambs are threatened and only rarely (Flerov and Gromov, 1935). Wandering dogs pose a positive danger to sheep everywhere.

---

[296] Sheep can run without perceptible slowing of speed for about one hour (Meklenburtsev, 1948).

Instances of attacks on sheep, including lambs, by golden eagle, lammergeier, and particularly by griffon vulture, have not been established beyond doubt; yet several investigators, based on information provided by hunters (Sarkisov, 1944; Antipin, 1947; Meklenburtsev, 1948), consider these birds enemies of sheep.

Wild sheep suffer from the same diseases as domestic sheep; mortality of wild sheep (in captivity or otherwise) has been attributed to necrobacillosis, Siberian ulcers, pasteurellosis, infectious pleuropneumonia, paratyphoid and other salmonelloses, pyrosepticemia, pyroplasmosis, and other diseases (Sarkisov, 1944; Sludskii, 1954). The death of mouflon due to Siberian ulcers was accurately diagnosed in two cases in the Crimean preserve (Rukhlyadev, 1939 and 1948); this same disease was the cause of wild sheep mortality in the Pamir in the winter of 1897/98 (Bronnikov, 1898; and others). An epidemic, which destroyed up to 50% of the population of wild sheep in some regions of the Pamir (goats, domestic sheep, and camels were also victims), was reported in the winter of 1886/87 but the disease never diagnosed (Golovnin, 1901; Meklenburtsev, 1948; and others).

Within the USSR alone over 50 species of helminths, including some 50 species in the Crimean preserve (Kadenatsii, 1958), have
652 been detected in wild sheep of the *Ovis ammon* group. Among Middle Asian argali sheep 32 species of helminths (27 species of nematodes, 3 cestodes, and 2 trematodes) have been identified, of which 27 are common to domestic sheep and several to other domestic animals. In just 15 individuals of *O. a. karelini* from the Chu-Ili mountains and Bet-Pak-Dala 28 species of helminths have been detected; some of these animals harbored up to 15 species of helminths simultaneously (Boev et al., 1948). Many of these helminths cause serious diseases, emaciation, and even host mortality. An intense infestation by *Skrjabinema ovis* affected 100% of the argali

sheep in Aksu-Dzhabaglin preserve. Among helminthic diseases in the Crimean preserve synthetocaulesis of the lungs and bronchi and dicrocoeliosis[297] of the liver are the two most serious and account for 18% of mouflon mortality from all causes (Rukhlyadev, 1939 and 1948).

Instances are known of wild sheep suffering from coccidiosis (Sarkisov, 1944; Svanbaev, 1958) and theileriosis (Rukhlyadev, 1948).

Skin mites *Hypoderma* parasitize wild sheep (their larvae form many fistulas on the skin of sheep); they suffer greatly from flies *Liperosia,* other dipterans, and various mites (Antipin, 1947; and others). In the Crimea six species of mites have been identified in mouflon (Yanushko, 1955). In several regions of Middle Asia argali sheep suffer from gadfly (*Oestrus ovis*) and mites (*Hyalomma plumbeum*) (Afanas'ev et al., 1953; Grunin, 1957). A large number of larvae of the nasopharyngeal gadfly in the nasopharynx of wild sheep is a common occurrence in Mongolia (Dordzhiin, 1958).

Scabies, caused by the mite *Acarus siro,* has been detected among wild sheep in Kirgizia, Kazakhstan, and Mongolia (Dubinin et al., 1958; A.A. Sludskii). Cases of mouflon in zoological gardens suffering from psoroptic mange, caused by the scab mite *Psoroptes,* have been recorded from time to time (Dubinin, 1955).

During snowy winters or winters with ice crusts a high mortality rate has been observed among wild sheep in the Crimea (Rukhlyadev, 1948), Pamir (Cheikin, 1914; and others), Chu-Ili mountains and Kazakh *melkosopochnik* (Sludskii, 1956), Altai (Pevtsov, 1883; Kolosov, 1939; and others), Sayans (Solov'ev, 1921), Mongolia (Bannikov, 1954), and so on.[298] Enfeebled sheep in such winters die of hunger or are killed by predators. In the Crimea sheep mortality was high in the cold and snowy winters of 1931/32 and 1939/40; in the latter year 40 carcasses were discovered in spring (Rukhlyadev, 1948). The winters of 1948 to 1950 were also snowy and extremely cold in the Crimea but large-scale mortality did not occur, possibly because the sheep population was relatively small and their pasture was not destroyed (Yanushko, 1955). In the severe winter of 1831/32 wild sheep perished completely in the Daurian mountains (Chir, Soktui, and others) (Radde, 1862), and individual survivors were eradicated in that year.

In the spring of 1942 in Aksu-Dzhabaglin preserve the bodies of

---

[297] The intensity of invasion by *Dicrocoelium lanceatum* may exceed 1,000 larvae (Rukhlyadev, 1948).

[298] Wild sheep mortality due to ice crust formation was seen in the winter of 1934 in Badkhiz but to a lesser extent (Heptner, 1956).

18 argali sheep were found at the site of an avalanche after it had thawed (Nasimovich, 1955). After a snowy winter fewer offspring are seen (Kashkarov, 1937; and others). Sheep weakened in snowy winters sometimes come close to human settlements or join herds of domestic sheep[299] (Sarkisov, 1944; Rukhlyadev, 1948). These animals can be caught in deep snow without difficulty (Solov'ev, 1921). Usually, even in normally severe winters, wild sheep by spring are highly enfeebled (Meklenburtsev, 1948; and others). References in literature to frequent cases of male mortality due to combats are apparently incorrect.

Domestic ungulates, especially small-horned cattle, are the most serious competitors of wild sheep, displacing them from the best pastures. Sometimes even during summer domestic sheep, goats, or
653 horses trample pastures on which wild sheep winter later. Argali sheep suffer more from helminthic infections than domestic ungulates, since the intensity of invasion is several times less in the latter (Boev et al., 1948). In most regions the importance of wild ungulates (mountain goats of the genus *Capra,* roe deer, kulan [onager], and others) as competitors of wild sheep is insignificant; [red] deer and roe deer might be competitors only in Crimean sanctuary where their population density is very high.

In the Crimean sanctuary, where predators (including wolf) are almost totally absent, the average number of lambs in summer in mouflon herds varies from 17.7 to 28.4% of the total population, with the average for a series of summers being 24.3%. The sex ratio is roughly equal: 46.6% males and 53.4% females. The annual increase in size of a mouflon herd over an 11-year period was 26.6% (Yanushko, 1955). The young comprise 17 to 33% of the total sheep population in Kyzyl-Dzhar (Badkhiz) (Heptner, 1956) and about 10% in the Trans-Ili Alatau (Sokolov, 1939). In regions with many wolves or places where sheep hunting is practiced, females are more numerous in the population than males.

Of 906 Turkmenian sheep caught between 1940 and 1942 in the central Kopet-Dag, only two males were eight years of age and none was older. Judging from the 187 pairs of horns of male sheep collected in this region in 1941 and 1942, only 1.0% of the total male population reached the age of seven years, 6.0%—six years, 15%—five years, and 28%—four years; the rest (50%) were under four years of age. Thus 93% were no more than five years old (Tsalkin, 1948 and 1951). In the montane gorges of Narym and Aksai, judging from

---

[299] Instances are known of the presence of argali in herds of yaks and horses (Dordzhiin, 1958).

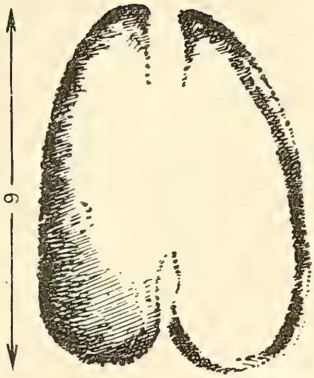


Fig. 221. Faint impression of the hoof of an argali in fine-grained soil in desert (reduced). Gobi Altai. August, 1926 (from Formozov, 1952).

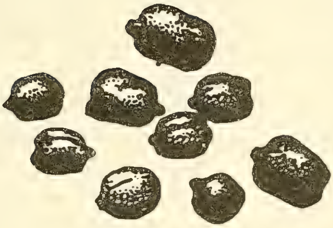


Fig. 222. Feces of mouflon (natural size). Crimean preserve. October, 1955. Sketch by T.L. Savranskaya.

skulls collected there, the majority of dead argali sheep were aged four to six years (Severtsov, 1873). In the eastern Pamir most of the skulls examined were of animals four to five years old; skulls of 12-year-olds (males) were found only twice (Meklenburtsev, 1948).

Field characteristics. Wild sheep are readily distinguished by external appearance from mountain goats and even more so from other animals. Males differ from females in their larger size, longer, heavier, and more intensely curved horns, much darker overall color, sometimes the presence of light-colored spots on the sides (in some forms they attain a large size and merge on the back into a "saddle"), and from the manelike tress of hair on the posterior part of the neck and chest, which develops in the second or third year. It is quite easy to distinguish the young up to 1.5 years of age from adults.

Frightened animals sometimes emit a whistling sound ("chshuu-u"), while the bleating of the young resembles that of lambs of domestic sheep. Adult males in rut snort.

In regions of permanent habitation of sheep well-beaten tracks rise gently into the hills and neighboring passes, pastures, solonetzes, etc. Beds are used over long periods (see section "Daily Activity and Behavior") and molted wool may be seen nearby. Nut-shaped feces are usually abundant, much larger than the feces of domestic sheep, with one end of the pellet somewhat pointed. Sheep chew grass right down to the roots.

654 "Hoofprints" are always evenly impressed, dew-claw marks are absent, and the toe more rounded than that of roe deer; the tracks of

males are larger than those of females (Shereshevskii, 1931; Formozov, 1952). (A.N.)

Economic Importance

Sheep are mainly hunted with either rifled bullets or buckshot (in the latter case the animals are quite often wounded rather than killed). The most common methods are by ambush or stalking at frequented places (water holes, salt licks, trails, and so on). Dogs are often used to keep sheep at bay on cliffs until the hunters arrive, and also to chase sheep past a stand, to drive them deep into snow, or to trail wounded animals. Specially trained dogs are used in the Pamir and in several other regions. If the terrain is favorable, the hunting party rides horses. Catching sheep in traps set up on their trails (Tadzhik, Kirgiz, and Kazakh Soviet Socialist Republics) is prohibited by law. Live animals are caught in nets, by chasing on snow, and in traps. Hunting is permitted (mainly with a licence) in autumn and early winter; in some cases only for males. In many regions hunting of wild sheep is totally prohibited (Crimea, Armenia, and others).

Only fragmentary information is available on the size of the harvest. In 1934 the Kirgizia Soyuzkozh (processing units) received 24,480 hides of argali sheep and mountain goats (in all, about 31,300 animals were caught). In two regions four tons of meat from the two species were supplied in a single year to the Forestry Department (Denisov, 1935). In the mid-1930's at one of the stations in the Trans-Alai range a team of military hunters procured seven tons of meat during the three winter months (Kuznetsov, 1937). In the early 1930's, according to the data of Zagotpushnina [administrative unit], about 4,000 hides of argali sheep were annually exported from the Pamir for processing (Rozanov, 1935). From this same region 3,500 hides of these sheep were prepared in 1937, with 1,500 to 2,000 of them contributed by the Alichur valley. Hunters annually killed 20 to 25 sheep with a gun; more experienced hunters killed up to 50 or more (Meklenburtsev, 1948). In the early 1940's in the central part of Kopet-Dag about 1,000 sheep were killed; of these, not less than 60% were females and young (Tsalkin, 1948). At the end of the 1930's and in the early 1940's the annual catch of wild sheep in the USSR exceeded 10,000; at present the catch is less.

The meat of wild sheep is best in autumn, between September to November until the commencement of rut (during the period of rut the meat of males acquires an unpleasant smell). The period of hunting is best limited to these months, with some variations in accordance with climatic and other conditions.

The meat of wild sheep tastes better but is inferior to that of domestic sheep from central Tien Shan in some quality indices. The yield of meat from Tien Shan sheep, *O. a. karelini,*[300] excluding the weight of horns is about 70%, or 6.0 to 6.5% less if horn weight is not excluded[301] (Denisov, 1935). Seasonal weight changes in Kopet-Dag sheep range from 10 to 15 kg or even more; weight differences among animals of a given age group may range up to 23 kg (Tsalkin, 1951).

The hide of argali sheep is of almost no value as a sheep skin because of the presence of about 85% dead hair, but is useful for processing into a hide (after chrome tanning, for making boots; the hide of young animals is converted into kid leather). Undressed hides serve as bedding material. Local people make skin bags for milk products, pack bags, cartridge pouches for saddles, and so on. Skulls and horns are placed between stones in building fences, and heavy horns used in horse lines as stakes or converted into utilitarian articles (Bulavin, 1934; Denisov, 1935; Meklenburtsev, 1948; and others).

655 Wild sheep have been domesticated. In the USSR (Armenia, Askaniya-Nova, Kirgiz Soviet Socialist Republic, and other regions) many experiments have been conducted for hybridizing the different subspecies of wild sheep (mouflon and argali sheep)[302] with domestic sheep (Askaniya rambouillet, merino, and fat-tailed sheep). As a consequence many breeds were evolved, for example mountain merino, arkhari merino, and others. One problem in these experiments was the development of breeds capable of grazing year-round in hills and yielding high quality wool and meat (Collection of Works on the Hybridization of Species) 1935; Sarkisov, 1944; Afanas'ev et al., 1953; and others.

Wild sheep readily adapt to domestication and thrive well in captivity. Corsican mouflon have been acclimatized in Askaniya-Nova where they are raised as domestic sheep. In the Crimea in 1913 mouflon (with an admixture of the blood of domestic sheep) were imported from Askaniya-Nova. They are well acclimatized there and are presently seen not only in the Crimean preserve but also outside it up to a distance of 50 km from the preserve borders (Yanushko, 1955; and others).

---

[300] The body weight of adult males of these sheep is 80 to 130 kg and that of females up to 60 kg or slightly more.

[301] The relative weight of horns of male argali sheep from the Pamir can reach 10% of total body weight.

[302] For example, in 1934 in northern Kirgizia 900 domestic female sheep (fat-tailed and merino) were inseminated with sperm from slaughtered argali sheep and 126 hybrid lambs obtained (Sb. *Vidovaya Gibridizatsiya* [Collection of Works on the Hybridization of Species] 1935).

In Armenia cases of damage to sprouting and heading cultivated plants caused by wild sheep have been registered (Sarkisov, 1944; Dal', 1949). Such damage has not been reported from any other region in the USSR.

Wild sheep require strict protection in many parts of the Soviet Union (A.N.)

22. SNOW SHEEP, BIGHORN SHEEP, CHUBUK[303]

Ovis canadensis Shaw, 1804

1804. *Ovis canadensis.* Shaw. *Naturalist's Misc.,* vol. 15, p. 610. Alberta, Canada.
1829. *Ovis nivicola.* Eschscholtz. *Zool. Atlas,* vol. 1, p. 1. Eastern Kamchatka.
1853. *Aegoceros* (*Ovis*) *montanus.* Middendorff. *Sibirische Reise,* vol. 2, pt. 2, p. 116. Polovinnaya River, tributary of Uda; Stanovoy mountain range. Nec Schreber, 1804 (American bighorn[304]).
1873.[305] *Ovis borealis.* Severtsov. *Izv. Obshch. Lyubit. Estestvozn., Antrop. i Etnogr.,* 8, 2, 153. Noril' mountains.
1904. *Ovis storcki.* J. Allen. *Am. Mus. Nat. Hist.,* vol. 20, p. 293. 110 versts east of Tigil fort in western Kamchatka.
1907. *Ovis alleni.* Matschie. Niedick's *Kreuzfahrten im Bering-Meer,* p. 236. Taiganos Peninsula, Okhotsk Sea.
1913. *Ovis middendorfi.* Kowarzik. *Zool. Anz.,* vol. 41, p. 443. Uda River valley.
1913. *Ovis borealis lydekkeri.* Kowarzik. *Zool. Anz.,* vol. 41, p. 443. 40 miles from the mouth of the Yana River.
1914. *Ovis lenaensis.* Kowarzik. *Peterm. Geogr. Mitt. Jrg.,* 1914, vol. 1, p. 4. Lena Basin. Nomen nudum.
1915. *Ovis nivicola potanini.* Nasonov. *Izv. I. akademii Nauk,* vol. 9,
656 p. 1599. Eastern part of basin of upper Zeya, Stanovoi range.[306]

---

[303] The first two names are bookish—translations from Latin ("snow sheep") and from English. The popular name "chubuk" is a slight variation of Yakutian "chubuku" or "chubukun".

[304] Middendorff, properly speaking, did not describe a new species of sheep but, having correctly judged the features of this form, placed it among the American species, giving it Schreber's name.

[305] Published in 1872.

[306] Sheep described from Stanovoi range. The same type locality has been accepted in this work. It is from here that the expedition of V.Ch. Dorogostaiskii brought

1923. *Ovis nivicola lydekkeri* forma *albula*. Nasonov. *Geografich. rasprostranenie gornykh baranov Starogo Sveta* [Geographic Distribution of Mountain Sheep of the Old World], p. 133. Verkhoyansk range.

1923. *Ovis nivicola lydekkeri* forma *obscura*. Nasonov. Ibid., p. 133. Tas-Khayakhtakh mountains, Yakutia. (V.H.)

Diagnosis

Sheep of moderate size and relatively heavy build. Flanks, back, and head of the same color, or else lightening occurs to the rear of the shoulders and on the head. Tress of hair from neck and upper part of chest absent. Horns very monotypic, fairly short, and invariably homonymous. Females also bear horns.

Bony core of horns short and thick (their length in adult males is less than circumference of base). Skull low and broad (width along posterior margin of orbit invariably greater than height). Cranium relatively long (length usually more than 43% of maximum length of skull). Facial part short. Nasals relatively short. Lacrimal depression shallow. (V.H.)

Description[307]

This species shows less geographic variability than argali sheep (*O. ammon*) but still it is significant, as is the case with American forms. Variability is relatively insignificant and exclusively restricted to color on the Asiatic mainland.

In general build snow sheep represent animals of compact and stocky build with a fairly massive trunk and a fairly thick, relatively short neck. Legs short and fairly thick. Head not large, slightly elongated, with small ears. On the whole, build less light and slender than that of argali sheep. Differences in the general appearance of the animals are particularly evident in their winter coat.[308]

Hair coat characterized by absence of bright rusty-brown and

---

sheep. In any case, such terms as "southwestern end . . . so called Stanovoi, or Yablonovyi range" (Nasonov, 1923), or "southwestern part of Stanovoi range" (Tsalkin, 1951) are no longer satisfactory and have not been employed here.

[307] More complete information about this species may be found in Nasonov, 1923; Flerov, 1935; and Tsalkin, 1951. These data, especially the latter's, have been used in the diagnosis and description. All data for the species, unless otherwise stated, pertain only to Asiatic sheep.

[308] The compact build of snow sheep, compared with argali sheep, is sometimes attributed to its living under very severe conditions (Allen's rule).

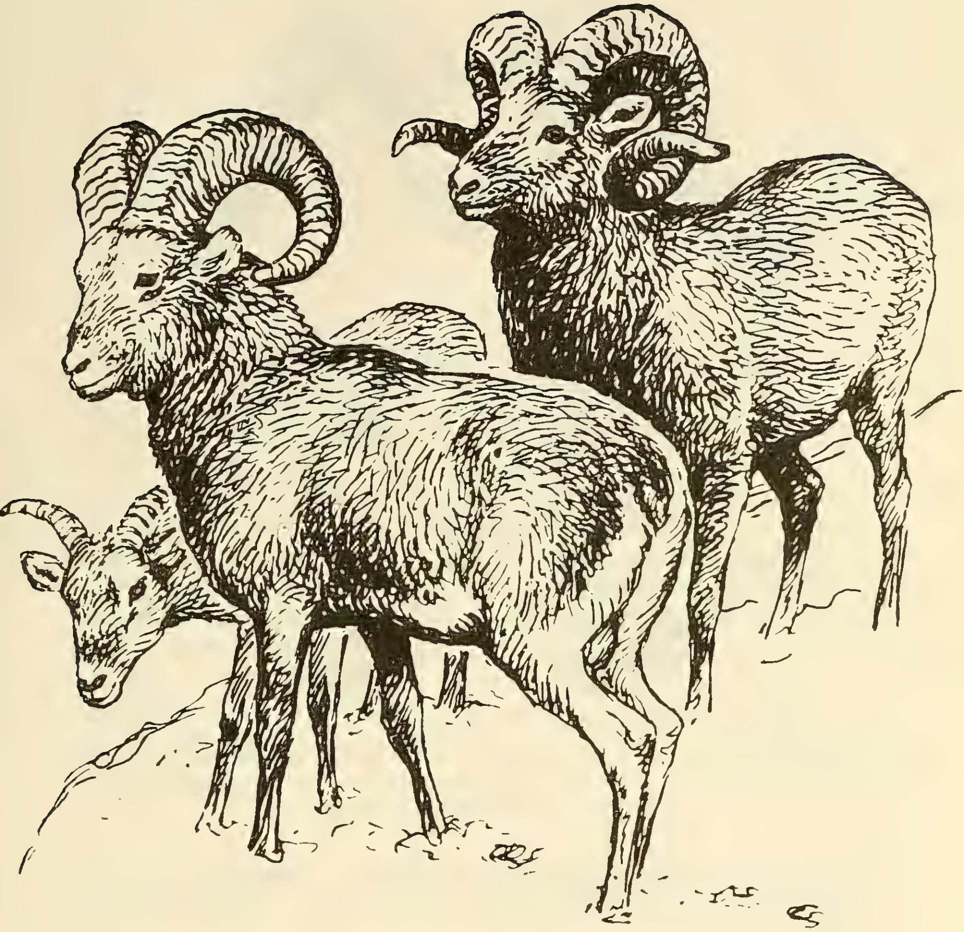
light yellow shades in general color and white saddle-type patches (some lightening occurs in other sections). Exhibits considerable geographic variability in coloration (see "Geographic Variation") but brown and cinnamon-brown shades are more typical. Tress absent. Winter coat very dense, long, and thick.

The color of Kamchatka sheep (*O. c. nivicola*) may be considered most typical of Russian forms. In winter the color is uniform and fairly monochromatic. General color shade on back and flanks varies from light yellowish cinnamon to intense cinnamon-brown. Along midline of the neck a small mane of elongated hair occurs, reaching the shoulders. Mane slightly darker in color than general body color. Abdomen, groins, and inner parts of limbs light, white, yellowish-white, or cream-colored. Much darker color of flanks merges into lighter areas of abdomen gradually, without a sharp boundary. Usually a slight darkening of overall color toward the rear of the shoulders is seen, but without boundary. Color of tail same as that of back. Relatively small white field present on sides and rear surface of thighs. Head either of same color as back and flanks or lighter, grayish-brown. End of muzzle and chin white or dirty white. Broad dark band occurs between end of muzzle and orbit, which is nearly the same color as the body or even a more intense cinnamon shade; band development highly variable and sometimes barely discernible. In some animals color on forehead and between horns lighter, 658 grayish-brown or dirty white (Tsalkin, 1951). Due to fading, general shade of color by spring may become very much lighter, resembling café au lait.

Coat color of females identical in winter and summer.

Horns of bighorn, compared with fully grown horns of argali sheep, relatively small in length (maximum length 111 cm). However, they are heavy and bulky. Bases are relatively thick and surfaces, especially frontal, broad. Frontal surface often appears to overhang temporal, as a result of which a small longitudinal depression or groove forms in the upper part of the temporal bone directly under the outer edge. Inner and particularly outer ribs well developed although somewhat blunt at times. Lower rib usually not formed. Frontal surface of horn flat, temporal bone (excluding groove) bulges slightly, and occipital bulges slightly at horn base but depressed at end. Horn surface relatively smooth; sharp transverse folds do not form and only small transverse prominences in the form of wrinkles present.

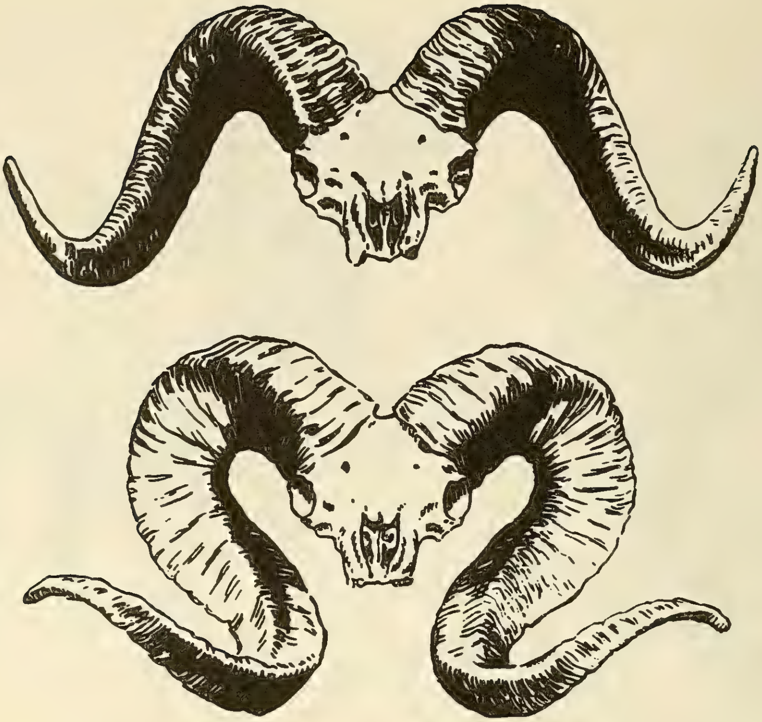
Pattern of twisting highly constant and invariably positive (outward), i.e., homonymous type. At the same time the curvature of the bend and other details may vary in individual animals and also at



657 Fig. 223. Kamchatka bighorn, *Ovis canadensis nivicola* Esch. Sketch by A.N. Komarov.

different ages. There are no significant geographic variations in horn structure among Russian sheep. Thus, while there are horns which are bent quite broadly and diverge highly sideways even in the first twist, there are also horns in which the spiral is extremely steep: the
659 horn in the basal and at the middle sections grows backward, downward, and inward, later forming the second spiral, turns steeply outward and extends almost horizontally, and bends only around its longitudinal axis.

The species under description is characterized by an extremely



658 Fig. 224. Extreme types of horn variation (partly age-related) among Kamchatka bighorn (*O. c. nivicola*). Animals 8 and 12 years of age. According to Nasonov (1923) and Tsalkin (1951) with minor modifications.

small first annual segment which disappears in adult animals. This segment is preserved throughout life among argali sheep (*O. ammon*).

Horns are invariably present in females and comparatively well developed. Their length ranges from 20 to 32 cm with a base circumference of 11.5 to 13.0 cm. A significant feature (unlike argali sheep) is their strong sideways divergence.

The skull of snow sheep is relatively low and broad, especially in the region of the orbits (its width along the posterior margin of orbits is more than its height), with shortened facial part, short nasals (their length is less than one-third total length of skull), and a relatively long cranium (length over 43% of maximum skull length). Depressions on lacrimals (lacrimal fossae) faint. Short, very thick horn cores are extremely characteristic. Their length is less than that of the skull while the base circumference of the core is more than its length.

In size snow sheep in the USSR are generally comparable to argali sheep of moderate size, i.e., Kopet-Dag sheep (*O. ammon cycloceros*), or slightly larger. Data on body size are extremely scanty. Three adult males (six to eight years old) from Kamchatka (*O. c. nivicola*) had a body length of 162 to 178 cm, tail length 10 to 14 cm, ear length 9.0 to 9.5 cm, and body weight 86 to 100 kg. Five adult females from the same region had a body length of 127 to 145 cm, tail length 10.0 to 11.5 cm, ear length 8.0 to 9.0 cm, and weight 46.9 to 54.1 kg. Large-sized individuals are much heavier, especially in autumn when they are very well fed. During this period males may weigh as much as 140 kg and females 60 to 65 kg. An individual was found in autumn which weighed 128.4 kg with 17.2 kg of fat (Yu. V. Averin, 1948). Females weigh one-half or even less than males. This proportion between the sexes is probably greater than in argali sheep (one-half).

Maximum skull length of males 255 to 300 mm and that of females 245 to 255 mm. On the average, length of skull of females only about 91% that of males. Length of bony core in males 150 to 270 mm and circumference at base 240 to 335 mm. Maximum horn length along curvature 111 cm but usually much less, and circumference at base 25 to 36 cm.

Other races of Soviet snow sheep, judging from skull size (information about other measurements absent) generally correspond in size to the Kamchatka race. (V.H.)

Taxonomy

Snow sheep represent a species which is more specialized than argali sheep (*O. ammon*; see "Taxonomy" under argali sheep). (V.H.)

Geographic Distribution

Bighorn sheep are found in northeastern and part of northern Asia and western North America.

Geographic Range in the Soviet Union

The range in the Soviet Union includes Pri-Baikal, Trans-Lena Siberia, central and northern parts of the Far East, including Kamchatka and Putorana mountains (Noril') on the right bank of the lower Yenisey. The range is thus divided into two unequal parts which are separated from each other, i.e., a small section in the Putorana and the main area covering eastern Siberia and the Far

East. At the same time distribution within the principal part of the range is extremely uneven. The animals are primarily associated with individual mountain ranges and upland regions or places with a rugged topography (cliffs on sea coasts); they are absent on the plains. However, even under these conditions there are significant gaps in distribution and animals are absent at places over large areas which appear quite suitable for their survival. Thus the range is divided into individual sections which, in some regions, are nothing 660 more than large pockets. In many cases separate places of occurrence of the animal are totally isolated from each other.

This situation is very largely associated with the extreme severity of conditions in which snow sheep live throughout their range. In particular, excessively deep snow prevents survival of the animal in some areas. Small absolute numbers also accelerate extinction of the animals over wide regions. Finally, for these reasons even the slightest thoughtless persecution could readily expose snow sheep to extinction. The latter would be all too easy since sheep inhabit large expanses on low, easily accessible mountains. Hence, in spite of human settlements being extremely sparse in the region of occurrence of snow sheep, the human factor plays an important role in the formation of its present-day range. At several places and in various regions absence of the animal or its random dispersion are the result of its destruction. On the whole, over a significant part of its range (especially in the south), snow sheep is dispersed more unevenly than argali sheep.

The Putorana (Syverma and Noril') section of the habitat is very small and occupies the central portion of the massif and the areas closely surrounding it. The area is bounded on the east by a line running from the upper reaches of the Romanikha River (entering the Kheta above Maimech) to the upper reaches of the Maimech and Kotui and farther encompassing the upper course of the Kochechumo. From there the boundary runs west, enclosing the watershed of the Kureika and lower Tungusk, and then forming the western boundary, goes north across the upper Khantaika and its watershed with the Pyasina, including in the distribution the montane regions of Lakes Kita, Glubokoe, and Lama. The northern boundary of the range coincides with the northern boundary of the uplands encompassing the upper reaches of Khata (Ayan and Ayakli). The range evidently includes the Noril' mountains, which represent the far western extremity of the entire massif and lie west of the above lakes (Nasonov, 1873; N.P. Naumov, 1934; Podarevskii, 1936). Thus the range falls roughly between 67° and 70°30′ N lat. and 88° and 90° E long. and has an irregular boundary; its length east to west and also north to south is about 400 km.

Information in literature on the occurrence of snow sheep in the Byrrang mountains in the Taimyr is erroneous. These animals are absent there and evidently were never present (V.G. Heptner). The range outlined above has obviously shrunk today. This is primarily true of its western part, i.e., the region of the Noril' mountains and the adjoining areas.

The main distribution (reconstructed) commences almost imperceptibly in the west somewhere in the region of the central or lower parts of the meridianal course of the Angara (region of Dolg and Shaman rapids; V.N. Skalon, 1949). From there it extends east through the upper reaches of the Lena to the northern Baikal district and the Patom uplands (Bodaybo region), to the Olekma-Chara upland, and the whole of the Chara basin. In the south the range extends somewhat south of the source of the Chara (Lake Leprinda) and its tributaries (the Tokko, for example) and reaches the Kalar region (Kodar range), i.e., roughly up to 56°N lat. (V.N. Skalon, 1946; Favorskii, 1936; Podarevskii, 1936). The range does not extend north of the left bank of Lena in this part of Siberia.

Farther east the boundary extends along the Stanovoi range, encompassing the sources of the Gilyuy, Great and Little Okonon, and Zeya on the southern slope of the range (Nasonov, 1923; Gassovskii, 1927). Even farther eastward the region of the Uchur basin (on the west, the Gonam and Algama Rivers and in the east, the Uchur) and the upper reaches of the northern tributaries of Uda (Polovinnaya) fall within the range. In this region the boundary shifts from the Stanovoi range to the Dzhugdzhur and Pribrezhnyi ranges extending along the Okhotsk coast. Snow sheep do not occur south of the Stanovoi range and are also absent in Tukuringr, in the Dzhagdy range (source of the Selemdzha), and in the Dusse-Alin slightly more to the south. On the Okhotsk coast, the Uda River and Uda garrison serve as the southern boundary of the range.

North of the Stanovoi range snow sheep occur in the Aldan-Uchur range, at least up to 58°(midcourse of the Gynyma River and
661 the left tributary of the Uchur,—the Neguskan and probably somewhat northward (Middendorff, 1853; Schrenk, 1858, Afanas'ev, 1934; V.N. Skalon, Shcherbakov and Bazykin, 1941; Nasonov, 1923). Thus the area of distribution under description represents a zone extending from the Angara to the Pacific Ocean.

North of the Stanovoi range the distribution of snow sheep encompasses almost the whole of the immense expanse between the Lena and the Arctic and Pacific Oceans.[309] However, there is no

---

[309] This part of the range has been taken from Skalon, Shcherbakov and Bazykin,

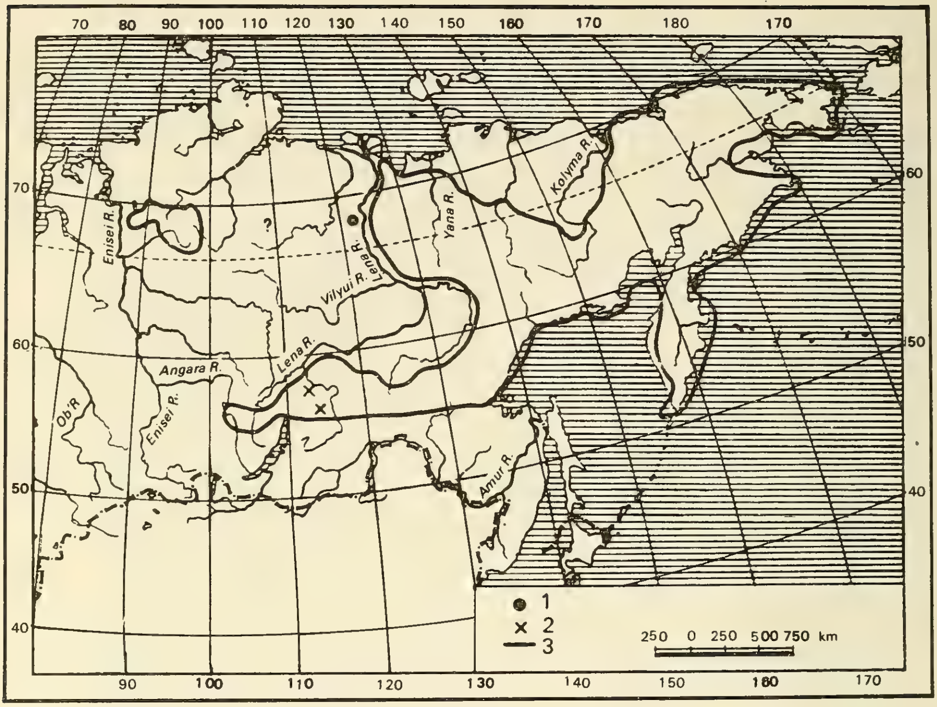


Fig. 225. Reconstructed range of snow sheep, *Ovis canadensis nivicola* Esch. in the Soviet Union (scale in km).

1—site on left bank of Lena; 2—present westernmost habitats in principal range (region of Bodaybo and Kodar range); 3—boundary of distribution. Question mark indicates probable occurrence of sheep in the region between the Lena and Khatanga. V.G. Heptner.

information about the presence of snow sheep in the region between the lower Olekma, parallel to the northern extremity of the Aldan-Uchur range, the Aldan, and the Lena; evidently, at least in the period under discussion, the animals were never there.

Elsewhere the distribution covers the Pribrezhnyi range throughout its extent, almost up to the coast of the Okhotsk Sea, the Dzhugdzhur range, Yudoma-Maya upland (especially the Allakh-Yunya basin), the entire Verkhoyansk range including the Kharaulakhsh mountains up to the ocean in the region of the Lena estuary and Buorkhaya Bay. The range does not extend to the left bank, west of the Lena. Only one report exists of snow sheep on the left bank,

1941; Belopol'skii, 1932; Dul'keit, 1927; Tugarinov, Smirnov and Ivanov, 1934; Sokol'nikov, 1927; Buturlin, 1913; Portenko, 1941; Samorodov, 1939; Bazhanov, 1946; and others; and from data on places of occurrence collected by Nasonov, 1923 and Tsalkin, 1951.

30 to 40 km away from the river at 71° N lat. between Govorov and Sektyakh (Skalon, Shcherbakov and Bazykin, 1941). Thus a gap of about 1,000 km or even more occurs between the area of habitation of snow sheep in the Verkhoyansk range and in the Putorana.[310]

In the Yana basin the range mainly covers the mountains in the upper and central parts of the basin and extends also up to the lowermost reaches of the river (snow sheep are known from a site 40
662 miles from the Yana estuary). On the lower reaches it covers evidently the mountains on the left bank (Kular ridge) and on the right bank (Poluosnyi ridge), at least the westernmost parts of the latter. The distribution includes all of the Tas-Khayakhtakh and several small massifs associated with it, for example the Andrei-tas, Mom' upland roughly up to 67°30', and montane regions south of the above mountain ranges in the upper reaches of the Indigirka and Kolyma (Nersk plateau, Kolyma upland, and others). In the east the range runs right up to the Sea of Okhotsk or the upper reaches of the rivers emptying into it (Okhota and others). On the left bank of the Kolyma the northern boundary of the range runs along its tributary the Ozhogina. The Alazeya plateau and the highlands associated with it on the right bank of the Indigirka do not fall within the range.

East of the Kolyma the range of snow sheep occupies the entire territory excluding evidently only the Yukaghir plateau. There is no positive information whatsoever about this part of the country. In this region the distribution includes the Kolyma range and its western spurs—the Kongir, Ushurakchan, and Oloy mountains, and the Southern and Northern Anyui ranges. It also covers Anadyr plateau in the region of the source of the Anadyr and its upper tributary (Eropol). Farther east the distribution covers the Chukot (Anadyr) range together with all the uplands associated with it, for example the Pakul'nei mountains, extending far south between the tributaries of the Anadyr, i.e., the Beloe and Tanyurer Rivers. In the region of the Kolyma estuary and on Chukot Peninsula the range extends up to the coast of the Arctic Ocean and to Bering Strait and the Bering Sea coast (Kresta Gulf, for example). The Anadyr lowland does not fall within the distribution.

South of the Anadyr the distribution of snow sheep encompasses all of the Koryak range, commencing from its northern spurs in the basin of the Anadyr tributaries, i.e., Maino and Bolshaya (Velikii) Rivers. The range extends here to the sea coast (Cape Navarin,

---

[310] The basin of upper Olen'ok is one of the lesser known regions in Siberia and could yield some surprises.

Shlyupochnaya, Glubokaya, and other bays, Olyutor Gulf, and the Goven Peninsula) and animals have been sighted at places even on coastal cliffs. Slightly west of the Koryak range, the distribution includes the mountains around Penzhina Bay (Penzhina range), mountains of the Taigonos Peninsula and the spurs extending west to Penzhin and lying in its basin (Ichigem range), and the slopes of the Kolyma range.

From the Koryak and Penzhina ranges the distribution directly merges into the Kamchatka mountains and includes all of the peninsula up to Cape Lopatka except for the lowlands on the west coast. The range extends in the east to the coast. It also includes the Altas Islands (Alagu and Araito), the northernmost of the Kuril Islands. Data for other islands here are highly tentative; it is possible that the animals inhabited some other northern islands.

At several places and over significant expanses of the reconstructed range described above, snow sheep are no longer seen today. Data concerning the Angara pertain to the seventeenth century[311]; today the animal is not seen west of the Bodaybo region and Kodar range.

Snow sheep are also absent in the Lena estuary and at several places in the Verkhoyansk range and adjoining uplands, the Tas-Kyayakhtakh range, and also in Anadyr territory. In Kamchatka the area of occurrence of snow sheep has shrunk, and they are extinct in Kuril Islands. It is, however, impossible to draw an accurate map of present-day distribution due to lack of adequate data.

Geographic Range outside the Soviet Union

The distribution outside the Soviet Union encompasses the mountains of Alaska in the north, including the Brooks range, in the west the Kenai and Alaska Peninsulas, the easternmost Aleutian Islands, and east to the Mackenzie mountains. The eastern boundary runs south-southeast along the eastern slope of the Rocky Mountains to the border of Canada and the USA. Later it turns sharply east and runs along the northern part of Montana roughly to the western boundary of North Dakota. From there it turns sharply south and, 663 running slightly west of the hundredth meridian, descends to northern Mexico. The southern boundary forms two southward projections encompassing, within Mexico, the southernmost parts of the Sacramento mountains and the northernmost parts of the western Sierra Madre. The range includes all of Baja California. The western boundary is formed by the Pacific Ocean (see Fig. 211).

---

[311] "Zhitie," [Life] of the Arch priest Avvakum.

At present the area of distribution of bighorn in America is still large but the animal has already disappeared from many places. It disappeared long ago from the Aleutian Islands and the Alaskan Peninsula (not Alaska state), and is absent in the Sierra Nevada and Cascade mountains and some places along the coast. (V.H.)

Geographic Variation

Geographic variation of this species, though significant, is not comparable to that of argali sheep (*O. ammon*). Color variability is quite high and dramatic among snow sheep and certainly not less, if not more, than in argali sheep. In addition to the color type described above, there are forms which are almost pure white (*O. c. dalli*), or blackish-brown, or almost black (*O. c. stonei*). Size variability also occurs but its magnitude is comparatively small and roughly corresponds to differences which are seen between argali sheep of moderate dimensions, i.e., Turkmenian type sheep (*O. ammon cycloceros*) and some larger types. Height at withers of the largest individuals of bighorn (*O. c. canadensis*) reaches 107 to 110 cm and body length 180 cm, i.e., their sizes approach those of rather small individuals of the Pamir group such as Tien Shan sheep (*O. a. karelini*). Weight of the largest American forms (*O. c. canadensis*) may reach in males 90 to 136 kg, maximum 156 kg, and in females 56 to 80 kg, maximum 108 to 109 kg. Some geographic differences are also seen in skull structure (some shortening of the facial part, which is very short in Asiatic forms) and some other features.

The horn structure remains surprisingly unchanged throughout the vast range. There is nothing remotely resembling their great transformation in argali sheep (*O. ammon*).

Views expressed long ago (Lydekker, 1913) about the composition of the species correspond wholly to the contemporary view adopted here. Nevertheless some recent researchers have split the species into two or even three species. The first group (Nasonov, 1923; and others) includes Asiatic species *O. nivicola* and some forms in America (*dalli, kenaiensis,* and *stonei*), which occupy the extreme northwestern part of the continent in the south to northern British Columbia. All remaining forms of American sheep have been placed in the species *O. canadensis,* which is thus not represented in Asia. Some American authors even now divide these two groups of American forms (*dalli* with proximate forms and *canadensis* with all the rest) into two species—*O. dalli* and *O. canadensis* (Cowan, 1940; Anderson, 1946; Miller and Kellog, 1955). These, together with Siberian *O. nivicola,* form three species.

Quite a large number of subspecies have been described within the species. In 1915 sixteen subspecies were recognized (Lydekker); since then more have been added (up to 20). Most pertain to American forms which show greater geographic variation than Russian forms. Within the Soviet Union variation is mainly restricted to change in coloration and sometimes absolute measurements of horns.

The following four forms might be recognized in the USSR but as yet have not been fully diagnosed.[312]

1. Kamchatka chubuk or snow sheep, *O. c. nivicola* Eschscholtz, 1829 (syn. *storcki*).

Maximum skull length in males 265 to 300 mm (M 280) and in females 245 to 265 mm (M 255). Horn sheath, larger in males, 170 to 270 mm (M 216) and circumference at base 250 to 335 mm (M 300). 664 Maximum horn length 11 cm and circumference at base 29 to 36 cm (M 32.5).

Color uniform, fairly dark, without significant lightening on flanks and head (see "Description").

Found in Kamchatka. Absent outside the USSR.

2. Okhotsk snow sheep, *O. c. alleni* Matschie, 1907 (syn. *montanus, middendorfi,* and *potanini*).

In size and skull and horn structure this form is similar to Kamchatka sheep (*O. c. nivicola*).

Color usually dark though fairly light-colored individuals are also known. Head, neck, and chest brown, tip of muzzle whitish, and nose bridge black. Forehead, space between horns, and occiput white. Trunk, especially flanks, lighter than neck, sometimes light brown. Dark band extends along spine. White spot present on flanks, behind axilla. In very light-colored animals this spot gradually merges with the light coloration of the shoulder blades, shoulders, and flanks. It is more sharply delineated in dark-colored individuals. In light-colored animals the dark band running along the lower flanks from the ulna to the groins is invariably distinct. Rear half of abdomen white.

Found in the Stanovoi range, Dzhugdzhur range, southwestern parts of the Kolyma range (Gydan), and mountains of the Taiganos Peninsula.[313] Absent outside the USSR.

---

[312] Very few individuals of these forms are found in museums; even the hides of some are not available. Complete data on weight and size of all the forms are not available in literature. The racial features given here are mainly from Flerov, 1935 and Tsalkin, 1951.

[313] Tsalkin (1951) also includes the Yablonovyi range in the geographic range of

3. Yakutian snow sheep, *O. c. lydekkeri* Kowarzik, 1913 (syn. *lenaensis, albula,* and *obscura*).

Skull size and structure same as in the forms described above, but bony horn core shorter and thinner. Length 150 to 210 mm (M 175) and circumference at base 250 to 280 mm (M 260). Horns much shorter and lighter; length up to 91 cm and circumference at base up to 25 to 33 cm (M 29).

Color very light, sometimes almost white or yellowish-white. Dark brown shades seen on cheeks, neck, chest, and front of legs. Dark-colored band extends along spine. Axillary space and bands running posteriorly brown. Lower portion almost wholly white or with some slight darkening in chest region. Front part of nose, forehead, nose bridge, tips of ears, and upper portion of neck light-colored or whitish. Top of head light-colored, almost white, without a dark transverse band on nose bridge.[314]

Found in Yakutia, from the Lena in the west (region of Verkhoyansk, Chersk, Mom', and other ranges), northern parts of the Kolyma range (Gydan), and Anadyr region.[315] Absent outside the USSR.

4. Noril' (Putorana) snow sheep,[316] *O. c. borealis* Severtzov, 1873.

Differences between this race and all other Siberian races are
665 almost unknown. In skull structure and measurements it evidently

---

this subspecies ("Yablonovyi and Stanovoi ranges," p. 274). These sheep are absent in Yablonovyi range, however, and were never present; they occur only in the Stanovoi range. This error is due to the fact that Dorogostaiskii and Nasonov (1915) and Nasonov (1923) considered Yablonovyi synonymous with Stanovoi ("Wild Sheep of Yablonovyi Range", 1915; "The so-called Stanovoi or Yablonovyi Range", 1923, p. 136; also see map). The orographic terminology of Siberia was not adequately developed in pre-Revolutionary Russia. At present, Yablonovyi range refers only to the chain running from the upper courses of the Olekma southwest through Trans-Baikal'ya.

[314] It is possible that fading of skin is responsible to some extent for extremely light coloration. In any case, this is definitely a very light-colored race, being the most light-colored of the Russian races and resembling to some extent the "white" sheep of America (*O. c. dalli*). These are distributed in Alaska, i.e., in parts of America which are closest to the Soviet Union and attempts have been made (Flerov, 1935) to establish a close relationship between them and the form described here. (V.H.)

[315] The question of the systematic position of sheep of Anadyr territory and Chukotka is not as yet clear. Also cloudy is the relationship between the Okhotsk form (*O. c. alleni*) and the Yakutian form (*O. c. lydekkeri*) in the Kolyma range and farther. It is possible that the former penetrates the north and northeast farther than is customarily assumed and even gets into Anadyr territory and Chukotka. (V.H.)

[316] The name "Taimyr," sometimes used for this sheep, is unsatisfactory and causes confusion; the reference is to the Putorana mountains (Noril') and not Taimyr. Sheep are absent in the Taimyr.

does not differ. Very little is known about its coloration since available material is negligible (only two rather unsatisfactory hides!). At the same time it is quite clear that in color this form is well distinguished from the Yakutian form (*O. c. lydekkeri*) and, evidently, also from the Okhotsk (*O. c. alleni*). Its color is dark and fairly uniform, resembling closely the Kamchatka form (*O. c. nivicola*). It not only occupies an isolated geographic range, completely separated from the rest of the range of the species in Siberia, but between it and the Kamchatka form yet another occurs—the Yakutian form (*O. c. lydekkeri*)—which is distinct in color and size of horns.[317]

This form is found in the Putorana (Noril') mountains.[318] Its range and that of the Yakutian form are completely isolated, apparently. Absent outside the Soviet Union.

In North America, as of now, 9 or 10 geographic forms of bighorn are usually recognized. This number is slightly less than it used to be but is still quite high.

The North American forms are as follows: *O. c. dalli* Nels., 1884 (Alaska, Yukon, Mackenzie, and northern part of British Columbia); *O. c. kenaiensis* J. Allen, 1902 (Kenai Peninsula, Alaska; sometimes included in the preceding form); *O. c. stonei* J. Allen, 1897 (northern part of British Columbia); *O. c. canadensis* Shaw, 1804 (Rocky Mountains); *O. c. auduboni* Merr., 1901 (Dakota, western Nebraska, and eastern Wyoming); *O. c. mexicana* Merr.,1901(south west Texas, southern New Mexico, Arizona, and northern Mexico); *O. c. californiana* Dougl., 1829 (from southern British Columbia to the Sierra Nevada); *O. c. nelsoni* Merr., 1897 (California to the south and east of the Sierra Nevada); *O. c. cremnobates* Ell.,1904 (southern California and northern Lower California); and *O. c. weemsi* Goldm., 1937 (central and southern Lower California).

American taxonomists usually place the first three forms in the species *O. dalli* and the rest in *O. canadensis*. Nasonov (1923) placed the first three among the Siberian species, *O. nivicola,* and the rest among the purely American *O. canadensis*. This group, in his opinion, bears features of similarity with argali sheep of the argali group (*O. ammon ammon*). One author (Cowan, 1940) states that the geographic range of group *dalli* does not adjoin that of the *canadensis,* and never did. (V.H.)

---

[317] Some elongation of hair over the groins, sometimes regarded as a characteristic of the Noril'ian form, should not be given diagnostic importance. This is a chance feature (molt) in one of the museum skins.

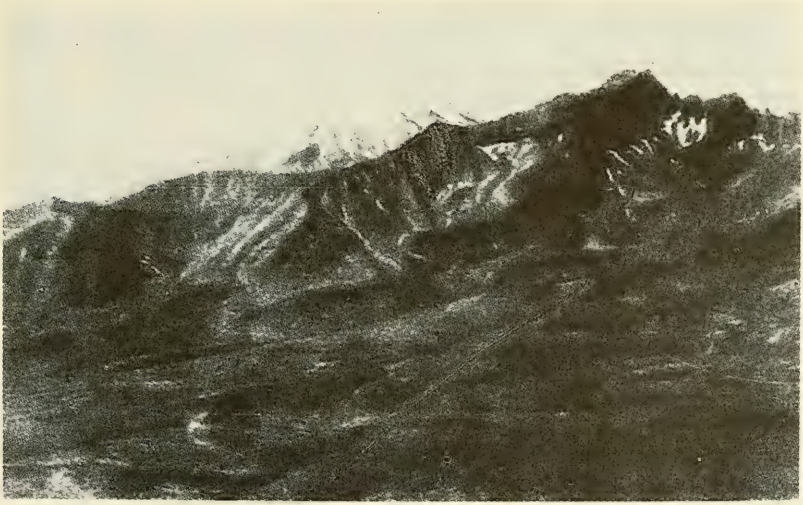
[318] The reference to "Taimyr and the mountains in the northern part of Siberia between the Yenisey and Lena" (Flerov, 1935) is incorrect (see "Geographic Distribution").

Biology

Population. Snow sheep are found in significant numbers mainly in Kamchatka, in adjacent Koryak land (Koryak national region), and in a few regions in northeastern Yakutia, for example the mountains of the Mom' River basin. These sheep are extremely few in numbers and at places almost extinct in the south (Stanovoi range), northwestern (Noril' mountains, Syverma range), and extreme northeastern parts of the range (Anadyr range and Chukot Peninsula). Stocks of snow sheep in many regions of northern and northeast Yakutia are also in a similar state (sheep disappeared a few decades back in the lower courses of the Lena and Kolyma).

In Kamchatka snow sheep are found in maximum numbers in Kronots preserve. At the beginning of the 1940's herds of some 60 animals were sighted and groups of 20 to 30 were not a rarity (Averin, 1951). In other parts of the range, as also in Kamchatka outside Kronots preserve, herds of 20 to 30 sheep were extremely rare; most often, a herd consisted of not more than 10 to 15 sheep. Some 50 to 100 years ago snow sheep were far more numerous everywhere.

Habitat. The habitat of snow sheep is a complex of inaccessible



666 Fig. 226. Summer range of snow sheep in montane tundra (alpine) zone in Shmidt volcano region. Kronots volcano visible in background. Kamchatka. August, 1946. Photograph by Yu.V. Averin.

cliffs, steep rocky, extremely rugged slopes, and relatively gentle
666 sections covered by pasture. On the whole, in the nature of its habitat and in some other biological features, these animals are more like mountain goats and differ considerably from sheep of the species *Ovis ammon,* which prefer a gentler topography. The vertical range of distribution varies from shore cliffs at sea level to the upper limit
667 of vegetation in the mountains. On Gamchen volcano (Kamchatka) snow sheep have reportedly been sighted at a height of 2,530 m, i.e., some 400 m higher than the last vegetation (Averin, 1948). These sheep avoid sites covered with forests.

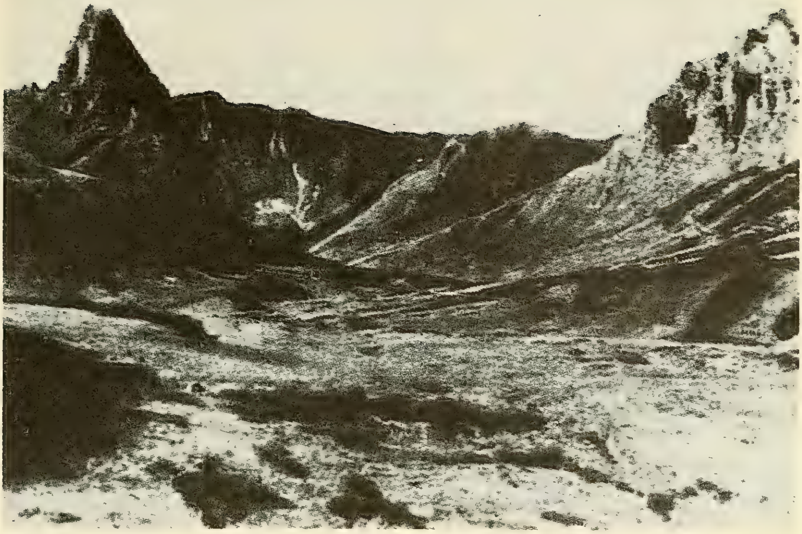
The following main types of habitat are characteristic of snow sheep in Kamchatka: 1) montane tundra (alpine) uplands where they are mostly found in the mountain belt from 1,000 to 1,600–1,800 m; 2) marine coastal escarpments (100 to 300 m) from where they sometimes descend almost to the sea; and 3) rocky sections of low mountain ranges and precipitous slopes of deep river valleys (500 to 800 m) where only small groups are seen (Averin, 1951). Sheep inhabit similar conditions in the mountains of the Koryak national region (Samorodov, 1939) and Kolyma River basin (Buturlin, 1913; and others). However, in view of the fact that the upper limit of vegetation is shifted downward here, sheep usually are not found above 1,200 to 1,300 m. In the mountains of northern Yakutia and also in the Stanovoi range these animals are distributed mainly in the montane tundra (balds) zone (Nasonov and Dorogostaiskii, 1915, Mikhel', 1937; Belyk, 1948). In the Noril' mountains and Syverma range they are found on low (up to 150 m) mountains covered by montane tundra vegetation (N. Naumov, 1934; and others).

Sheep hide from predators in the cliffs and emerge for grazing on open slopes. In some regions adult males in summer are confined to slopes at a level higher than that of females and young (Averin, 1951).

Food. Nutritional characteristics have been studied only in a general way. Up to 50 plant species are known to be consumed by snow sheep in the Soviet Union, including no less than 40 species[319] in Koronots preserve, of which roughly one-half are avidly consumed in any season. These include: rushes, sedges, willow, locoweed *Oxytropis*, grasses (meadow grass, mountain fescue, and reed grass), heathers (mainly in winter), sagebrush wood, club moss *Lycopo-*

---

[319] Species identification of lichens (and also mosses) consumed by Kamchatka sheep has not been done. In the Penzhina basin sheep consume *Cetraria nivalis* and *Cladonia alpestris* (Tsalkin, 1947) and in the Stanovoi range *C. rangiferina* (Nasonov and Dorogostaiskii, 1923).



666 Fig. 227. Summer range of snow sheep in Shmidt volcano region. Kamchatka. August, 1946. Photograph by Yu.V. Averin.

667 Fig. 228. Habitat of snow sheep in southern part of Kharaulakh mountains. Gorge at sources of Kyutyur River. June 20, 1955. Photograph by V.V. Kapitonov.

dium (in winter), saxifrage, and partridge grass (only in summer), etc. Berry shrubs are also consumed: blueberry, mountain cranberry, crowberry, and bearberry *Arctous** *alpina* (Gavrilov, 1947; Averin,
668 1951). In the mountains of Anadyr territory the favorite foods of sheep are spleenwort *Asplenium* and mountain rue *Ruta muraria* (Sokol'nikov, 1927). In the Stanovoi range, when mushrooms appear, sheep quite often descend into the forest to eat them, remaining there only long enough to feed, climbing again to the balds when finished. In addition to willow, sheep also eat the leaves and shoots of birch (*Betula fruticosa*) and other shrubs (Nasonov and Dorogostaiskii, 1923).

In Kamchatka grazing on green fodder continues for 4.0 to 4.5 months (from June through October); standing dead material, terrestrial lichens, and willow constitute the main foods in the remaining period. Not only are dead vegetation and lichens consumed, but sheep actively dig them up from under the snow with their hooves when the snow cover is not too deep. In winter, especially when the snow is very thick or on days of snowstorms, sheep exhibit no selectivity and consume almost all accessible plants, biting off the stalks right down to the base (Gavrilov, 1947; Averin, 1948 and 1951). In winter the food ration of snow sheep is similar to that of reindeer.

The maximum weight of the stomach contents in summer may attain 7.8 kg in adult females and 10.8 kg in males; in winter the corresponding values are 4.3 and 4.7 kg.

The species composition of food plants of Kamchatka sheep is extremely similar to that of *O. c. dalli* occurring in the interior of Alaska. Among the winter foods of sheep in McKinley National Park are moutain cranberry, crowberry, partridge grass, and saxifrage,[320] along with grasses, sedges, willows, and sagebrush. Willow twigs (thickness up to 0.5 cm) and leaves are also consumed. Sheep descend to river beds in October and November in search of willow leaves which remain green for a long time. Not only the green parts but also the berries of berry shrubs are consumed; blueberry is their favorite (Murie, 1944).

Snow sheep regularly visit dry salt licks (Nasonov and Dorogostaiskii, 1915; Belyk, 1948; and others). During some periods of the year their feces consist almost wholly of clay (Murie, 1944). Sheep rarely visit water holes.

Home range. The home range has not been accurately established. Compared with *O. ammon,* snow sheep lead a more settled life and wander within very narrow confines; in Kronots preserve they do not emerge throughout the year beyond the limits of a given volcano or mountain range. In winter they are confined to a far more restricted area than in summer (Averin, 1948 and 1951).

---

[320] According to Averin (1951) the last two species are consumed only in summer; this is apparently incorrect.

*=*Arctostaphylus*—Sci. Ed.

Daily activity and behavior. In summer only part of the daylight period is spent in grazing, with rest and rumination occurring at intervals. In the evening the animals return to cliffs. In the Stanovoi range sheep graze most actively in the morning and evening, lying down most of the day; normal daily rhythm is disturbed by rain or bad weather. To protect themselves from midges, sheep move onto open, wind-blown slopes (Nasonov and Dorogostaiskii, 1915). In Kronots preserve old males ascend the slopes at night and conceal themselves among the rocks. In winter sheep graze from dawn to twilight. They avoid sections with deep powdery snow cover and for winter wanderings use mountain crests and slopes where the snow attains high density. They prefer to use the same trail (Averin, 1948 and 1951).

Sheep easily negotiate steep slopes and clamber well along cliffs; females usually move more rapidly and dexterously than heavy males. Sheep are usually credited with excellent vision and less developed auditory and olfactory faculties (Nasonov and Dorogostaiskii, 1915; Sokol'nikov, 1927).

In summer adult females and males live in different herds; some males live singly or in small (up to four or five animals) groups. Juveniles in their second year stay with the females. Commencing from the end of August, but mainly in October, mixed herds form. Mixed groups are common throughout winter[321] and break up in May to early June. Herd composition is not constant and groups
669 mix readily in common grazing grounds but split up later. The herding instinct is apparently maximum in autumn, before estrus, and in winter. In the USSR, except for the territory of Kronots preserve, snow sheep herds of over 20 animals are very rare.

Seasonal migrations and transgressions. Seasonal wanderings are not very prominent, characterized by short (less than 10 km) distances, and occur usually within a given mountain range.[322] In most regions sheep are confined in winter to a slightly lower level than in summer[323] and congregate on steep rocky slopes which are very windy. In the snowy mountains of Kamchatka they are never

---

[321] The statement that males and females winter in separate areas in the Stanovoi range (Nasonov and Dorogostaiskii, 1915) is apparently erroneous.

[322] In Alaska sheep wander up to 16 km.

[323] In Penzhina Bay some sheep remain in winter at a slightly higher level than in summer since higher levels are more windy (Tsalkin, 1947).

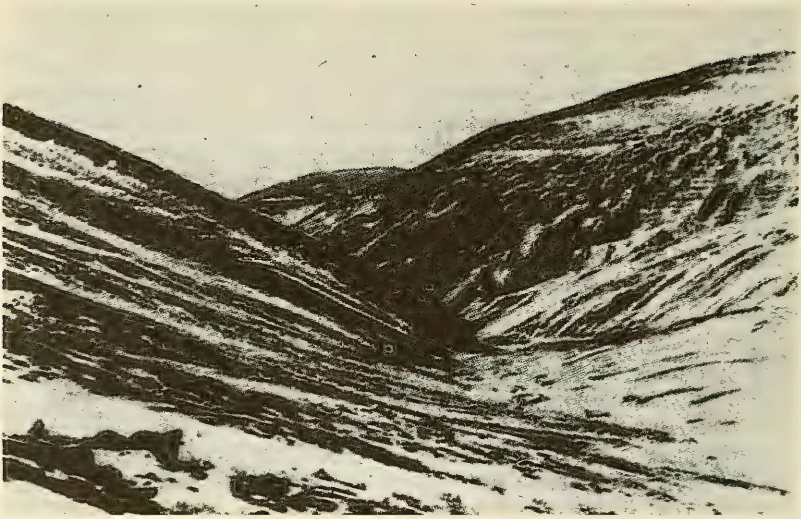


Fig. 229. Autumn range of snow sheep in the Kharaulakh mountains. Upper course of Ortokuukhta River (Lena basin). October 7, 1956. Photograph by V.V. Kapitonov.

found in forests in winter. They prefer the upper regions of sparse larch forests in northern Yakutia, evidently because the snow cover there is not so deep in winter (Mikhel', 1937; Belyk, 1948). In Kronots preserve mountains and volcanoes adjacent to one another usually boast several fairly isolated wintering sites connected by trails (Yu.V. Averin).

Migration to wintering sites occurs in different regions from the end of August to October inclusively. In spring, with the onset of thaws, sheep gather on southern slopes (Stanovoi range). In the Geizer River valley of Kamchatka, there is less snow in the proximity of active geysers and grass begins to grow early. Hence snow sheep are seen quite often there in spring. Sheep wintering on coastal escarpments of eastern Kamchatka descend in May to bays where green vegetation has sprouted. In the second half of June they depart and reascend slopes. Toward the end of June and in early July even sheep wintering above timberline move higher into the mountains (Plechev, 1939; Averin, 1948).

The attraction of snow sheep for rocky topography is particularly distinct during migrations. Alaskan sheep in moving across relatively level areas select for crossing rivers, banks which are 670 extremely stony and apparently less convenient for movement, areas surrounded by rocky ledges, or minor elevations, and so on (Murie, 1944).

Reproduction. Information on rut given in Soviet literature is based on data provided by hunters. Sheep are polygamous. In the Noril' mountains, northern Yakutia, and Kamchatka, sheep come into rut from the second half of November to the middle of December.[324] In rare instances mating has been observed even at the end of October (Averin, 1948). During the period of rut sheep live in mixed herds consisting of females, juveniles, and one or more adult males.

Combats between males are relatively rare. Instances are known of a single female being chased by four males simultaneously. Judging from the periods of parturition, rut may continue for a very short period (in Alaska for two weeks; Murie, 1944) or be prolonged (in Kamchatka, over one month; Averin, 1951). The period of rut depends on weather conditions and how well fed the animals are. Males become visibly enfeebled during the period of rut.

References to the time of onset of sexual maturity are contradictory. Probably some females mature in their second year, but most reproduce only in the third autumn. Males mate only after three years. American bighorn (*O. c. canadensis*) mature in their third autumn (Trippensee, 1948).

Gestation lasts about six months and lambing occurs from the end of May to mid-June. In Alaska significant variations have been noted in the periods of parturition in different years (Murie, 1944). Before giving birth females isolate themselves from the herd and go to a concealed site. Females deliver a single lamb.[325] In Kronots preserve all 19 of the pregnant snow sheep autopsied contained only one fetus. An ewe with two lambs has not been observed in herds (Averin, 1951).

In Kronots preserve up to 10% females remain barren (Averin, 1951).

Growth, development, and molt. Lambs initially remain crouched in the grass and begin to follow the ewe when roughly one week old. In Kronots preserve suckling females are seen up to September 18 but no milk was found in the stomachs of some lambs even in early August (Averin, 1951). In Alaska a lactating female was sighted in February. Lambs begin to nibble at grass when they are 7 to 10 days old. Juveniles remain with their mother for 1.0 to 1.5 years (Murie, 1944).

---

[324] The statement that these animals in the Stanovoi range rut in the latter half of September (Nasonov and Dorogostaiskii, 1915) is obviously erroneous.

[325] There is a reference to female snow sheep on occasion delivering twins in south Kamchatka (Plechev, 1939). It is possible that this information is based on some misunderstanding.

Weight of newborn lambs is not known. Two lambs caught in Kronots preserve in early August weighed 13.5 (male) and 20.8 kg (female). At the age of 14 to 15 months Kamchatka sheep weigh 30.6 to 42.0 kg (three animals). Depending on the season and their fatness adult females weigh 45.5 to 54.1 kg (eight animals) and males 53.0 to 128.4 kg (six animals). The weight of the largest animal may apparently reach 60 to 65 kg (females) and 140 kg (males) (Averin, 1948 and 1951; Gavrilov, 1947).

In the first year of life the horns grow for not more than three months and hence the length of the first segment averages only 28% of that of the second (or 66 to 70% in *O. ammon* living under less severe conditions). Juvenile hyaline horns evidently do not grow at all. The most intense horn growth occurs in the second year. The diameter of horns in females continues to increase for three or four years and in males up to six years (usually only up to four or five years in males of *O. ammon*) (Tsalkin, 1951).

Lambs, compared with adults, have a duller, grayish-brown color; they have no elongated hair on the upper part of the neck (Tsalkin, 1951).

In Kronots preserve the wool of adult sheep falls out readily even in the latter half of February. True molt apparently commences in
671 April, peaks in May and June, and ceases only by early August or even later. Molt starts from the legs and abdomen; winter hair is retained longest on the head between the horns. Dark summer wool is evident from the latter half of June to early July. The first to molt are adult males and females without offspring, and the last are females with lambs and emaciated animals. Winter wool begins to grow from the second half of August. By November the winter coat has attained normal length. In the Stanovoi range sheep molt into their summer coat in the first half of July, i.e., a few weeks earlier than in Kamchatka (Averin, 1951; Ditmar, 1901; Nasonov and Dorogostaiskii, 1915).

Enemies, diseases, parasites, mortality, competitors, and population dynamics. Wolves and severe winter conditions are of utmost importance among the various factors responsible for sheep mortality. Very large numbers of sheep are killed by wolves in winter when the predators hunt in packs and sheep are highly emaciated because of nutritional deficiencies. In McKinley National Park (Alaska) wolves are common and destroy mainly sheep up to two years of age and those older than eight years. In 1,174 feces of wolves examined, sheep remains were detected in 25.9% (Murie, 1944). In some wintering sites of snow sheep in Kamchatka feces of wolves consisted wholly of the remains of these ungulates. In summer, as a result of migration of wolves into the forest zone at lower elevation, sheep are less endangered by them (Averin, 1948 and 1951).

Among other predators of sheep, wolverines persecute them mainly in winter and are very dangerous; however, the wolverine population in most montane regions is insignificant. Third place is held by occasional enemies such as lynx, bear, and golden, white-shouldered [Steller's sea], and common [white-tailed sea] eagles [*Haliaeetus pelagicus, H. albicilla*]. Bear and predatory birds mainly attack the young. Possibly the white-shouldered eagle (*Haliaeetus pelagicus*) attacks lambs more often than other predatory birds (Samorodov, 1939; Averin, 1951). In Alaska the remains of sheep were found in 15 of the 632 nests of golden eagle examined, but carrion should be considered the main source (Murie, 1944). In Kronots preserve lamb remains have been found twice in the feces of bear (Averin, 1951).

The diseases and parasites of east Siberian and Kamchatka snow sheep have not been studied. The various forms of American bighorn suffer from pasteurellosis, actinomycosis (agent—fungus *Actinomyces bovis*), necrotic stomatitis (agent—*Actinomyces necrophorus*), scabies (agent—mite *Psoroptes communis*), and protostrongylosis. Actinomycosis takes a chronic form, while stomatitis sometimes results in the death of young animals (Murie, 1944). Epizootic protostrongylosis, caused by *Protostrongylus s[t]ilesi,* leads to pneumonia, which time and again has been the cause of death of several hundred bighorn in different parts of the USA; in some cases over 90% of the local population died in a single winter. The spread of the disease was facilitated by deteriorated conditions in the habitat, due to a reduction in suitable wintering sites, and acute competition from other species of ungulates (Buechner, 1956; Honess and Winters, 1956; McCann, 1956; and others).

Even in preserves a very large number of sheep die before their eleventh year. In McKinley National Park (Alaska) among the 829 skulls of sheep examined, four belonged to 12-year-old females and three to 14-year-old males. In the latter the teeth were completely worn out (Murie, 1944).

Lambs are particularly threatened by severe winter conditions and resultant malnutrition, emaciation, and predatory activity of wolves. In McKinley National Park (Alaska), of the 829 sheep skulls examined, 158 were animals up to 1.5 years of age. In this region severe mortality among sheep, mainly young and old, was observed during the severe winters of 1928/29, 1931/32 and 1939/40; these winters were characterized by excessive snow, formation of ice crusts, and prolonged snowstorms. In the course of the winter of 1928/29

the bighorn population of McKinley National Park fell by one-
672 third. In the winter of 1931/32 mortality was much higher. Following this winter many females did not reproduce (Murie, 1944). In Kamchatka sheep wintering close to the sea experience time and again great difficulties due to ice crust formation (Plechev, 1939).

Only wild reindeer can be considered a competitor of snow sheep in the USSR, but the wintering sites of the former do not coincide, since snow sheep winter in large numbers at higher elevations and on much steeper slopes (Averin, 1951).

In herds of American bighorn (*O. c. canadensis*) the ratio of adult males to females varies from 1 : 3 to 2 : 3, i.e., females predominate (Buechner, 1956). Some females lose their lambs within the first few days of birth. A significant number of lambs (on the average about 50% of those attaining the age of several weeks) perish mainly during their first winter before completing their first year (Averin, 1951; and others).

Field characteristics. In external appearance snow sheep are readily distinguished from other ungulates, i.e., reindeer and musk deer which are sometimes encountered in the same habitat. Male sheep differ from females in their much larger build and powerful horns; color differences, particularly in winter, are insignificant. The presence of sheep can be judged from well-beaten trails, abundant feces close to rocks, and tufts of light-colored molted wool adhering to bushes. The voice of adult and young bighorn is somewhat higher pitched than that of domestic sheep (Yu.V. Averin). (A.N.)

Economic Importance

In the Okhotsk-Kamchatka region the commercial export of snow sheep hides from 1891 to 1912 through Petropavlov-on-Kamchatka varied from 115 to 576 pieces; 1,780 hides passed through the city of Okhotsk in 1912 (Emel'yanov, 1927).

According to pripolar records for 1926 and 1927 the annual catch of snow sheep in the Verkhoyansk region was 1,771 animals; in the Far East—1,611 (including 486 from Petropavlov region, 390 from Okhotsk, 329 from Penzhina, etc.), and not more than several dozens from other regions in the country. These figures are considered underestimates. In the mid-1930's no less than 2,000 snow sheep were caught annually in northern Yakutia, mostly the northeastern regions, and up to 7 to 15 animals by each household (Mikhel', 1937). In the first half of the 1940's no less than 500 were caught in east Kamchatka and 800 to 1,000 throughout Kamchatka (Averin, 1951). Compared with trade in other species of animals for their meat, snow sheep in Kamchatka occupied third place in the 1940's, following wild reindeer and bear (Averin, 1951), and second or third place in several other regions of the Far East. In the Mom' region of Yakutia snow sheep used to be a chief object of trade of the Evenks (Skalon et al., 1941).

At present snow sheep serve almost exclusively as an object of commercial hunting. Nowadays hunting these animals is limited to certain periods, catching of females prohibited, or hunting totally banned. The produce is used exclusively by the local population and has almost no commercial value.*

Snow sheep are caught mainly in autumn when the quality of the products is superior and hunting more rewarding. Hunting is practiced by stalking or by lying in wait for them on their trails. In the Stanovoi range dogs are used in hunts. They chase the sheep onto rocky ledges ("otstoi") and keep them at bay until the hunter arrives (Nasonov and Dorogostaiskii, 1915). Near the sea shore in the Far East, hunters climb from the seaward side onto cliffs where sheep live. In some regions of Yakutia, up to the 1940's snow sheep were caught by setting up automatic traps in their trails.

Among the products of snow sheep, meat and hides are particu-
673 larly valuable. The quality of meat is mostly superior in autumn; at that time of year the meat of year-old females and young is particularly tasty. In autumn adult sheep may yield up to 10 to 15% fat reckoned on body weight. In the Gizhiga region a large sheep used to yield about 60 kg of dressed meat (Arsen'ev, 1925). In the period of rut the meat of adult males acquires an unpleasant taste; in winter it is very lean.

Hides of snow sheep are used in sleeping bags (they are warmer than those stitched from hides of reindeer, wolves, or dogs), leggings, and beddings. Sometimes they are converted into chamois leather. Hides of sheep caught at the end of September to early October, when the hair is not yet fully grown and hence less brittle, are best for making sleeping bags (Averin, 1951; and others). Horns are used as decorative trophies or converted into ladles, combs, knife handles, small scoops, tubes, buttons, and various other articles.

It is desirable to conduct experiments on the hybridization of snow sheep with domestic sheep[326] in order to develop a new strain of sheep well adapted to the severe conditions of the north. Snow sheep should also be released in new regions in order to expand their range (Flerov, 1935; and others).

---

*Statements regarding the commercial value of bighorn appear somewhat contradictory in this paragraph—General Editor.

[326] Experiments conducted in the USA have shown that these species crossbreed well.

The continuing reduction of snow sheep populations, their total disappearance from some regions in the north Kuril chain, some regions of southern Kamchatka, the lower courses of the Kolyma, southern Yakutia and southwestern parts of the range, make obligatory more stringent hunting regulations. The hunting season should be restricted to September, October, and the first half of November. (A.N.)

Supplement to Order of Even-toed Ungulates

Artiodactyla

DEER FAMILY

Family CERVIDAE Gray, 1821

Genus of True Deer
Genus *Cervus* Linnaeus, 1758

23. FALLOW DEER[1]

Cervus (Dama) dama Linnaeus, 1758

674 1758. *Cervus dama.* Linnaeus. *Syst. Naturae,* 10th ed., vol. 1, p. 67. Southern Sweden (acclimatized).

1798. *Cervus platyceros.* Cuvier. *Tabl. èlém. de l'Hist. Nat. des Anim.,* p. 160. Renamed *Cervus dama*[2] Linn.

Diagnosis

Small-sized deer with spotted pattern on the body at all ages, a relatively long tail, and antlers without bez tine. In most cases a well-developed or prominent vertical palmate portion occurs at the end of the antlers. Nasal bones poorly enlarged posteriorly and with deep notches at the anterior end. Nasal processes of premaxillae narrow. (V.H.)

Description

Build typical of members of the genus but lighter and more slender than that of red deer, and even more so than that of sika. Body fairly massive and legs relatively low. Fore part of body somewhat shorter

---

[1] In hunting literature fallow deer are sometimes called "daniels" or "danielks"; in olden times they were also called "danilks".

[2] Further synonyms are not of interest and are mainly based on color variations. A complete list is given by Miller (1912), Lydekker (1915), and Ellerman and Morrison-Scott (1951).

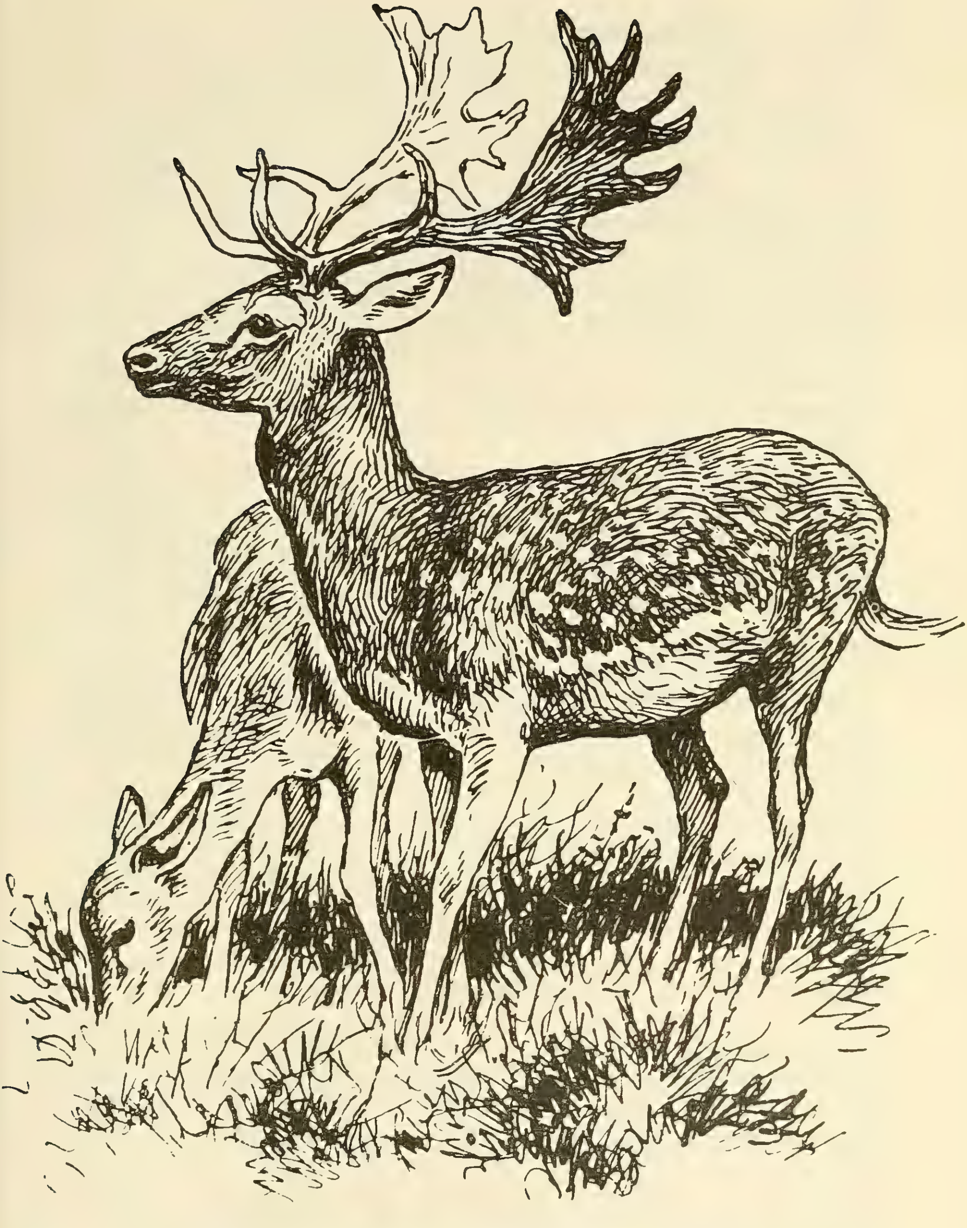
than the rear and sacrum slightly higher than withers. Back straight, its contour rising slightly rearward. Neck fairly long, head relatively short and high, significantly narrowing anteriorly, with a broad and flat frontal region, and wide-set eyes. The animal holds its neck and head high. Tail long, much longer than the ears, and thick. Bare section on nose small and covers region from the upper lip to the
676 nostrils; top of nose between nostrils covered with hair. Ears relatively short with pointed tips. Eyes large and dark.

Hooves of middle digits fairly large and elongated while hooves of lateral digits very small (smaller than in other Russian species of the genus) and set high; they do not touch the ground even on soft soil. Rear hooves joined with a skin flap only in the rear portion.

Antlers of moderate size, set fairly steeply from the brow and third tine, but without ice [bez] tines. Tips of antlers with well-developed, short, vertically set palmate portion ("shovel") with distinct, mostly short, processes along its rear margin. Palmate portion has no processes which are set forward. Sometimes palmate portion barely visible or even not developed, but apical processes are nevertheless set backward. Sometimes even lower portions of horns tend to enlarge and flatten.

Hair on neck shorter than on trunk but hair on dorsal sides of neck elongated and forms something like a short mane. There is no true mane or beard. Hair from withers to occiput set forward, giving the impression of a reverse nape. Tuft of long hair occurs in genital region.

General color of summer coat rusty or brownish-rusty, much darker toward the back and becoming lighter ventrally. Entire ventral surface, apart from lower portion of neck, and medial and posterior portions of extremities white. Along middle of the back color generally darker and a dark-colored stripe extends down the center. Toward the rear color turns blackish and is black or almost black on croup. Small white speculum present on rear of thighs in region of tail; it does not extend onto croup. From sides and top speculum fringed in black. Toward the top these black sections merge with black stripe on croup. Tail white with a black median band. This coloration of tail together with black-and-white speculum results in a bright and prominent body section. On the flanks, shoulders, and thighs numerous discrete light-colored spots occur. They form a regular row along the sacrum; a similar row, often fusing into band down the flanks, forms the border of the region covered with spots. Ventral surface of neck white or whitish. Head generally rusty or brownish-rusty color, tip of muzzle along edge of mouth whitish, inner surface of ears white and outer rusty, and a light-colored ring



675 Fig. 230. Fallow deer, *Cervus dama* L. Sketch by A.N. Komarov.

encircles eyes. There are no sex-related color differences.

Winter coat much longer, denser, duller, and uniform in color than summer coat. Its general color is rusty or grayish-brown. Spots present but faint and sometimes invisible, especially at end of winter. Juveniles rusty-colored with distinct spots.

Fallow deer in Europe have for long remained essentially domestic park animals to a far greater extent than any other species of deer. As a result, variability in coloration is high among them; they exhibit melanism and albinism, especially the latter. Albino animals are very common at some places and even form small populations.

Preorbital gland small but forms a deep sac. Hoof gland of forelimbs lies between hooves in a deep groove with a hairy skin. On the hind limbs glandular opening moderately deep. Tarsal gland well-developed and located beneath calcaneal joint. Dense elongated hair covering it forms a pad and due to white coloration is very prominent.

Skull broad, especially in the region of forehead, and somewhat flattened. Nasal bones long and pointed posteriorly; posterior ends reach level of anterior margin of orbit and even extend behind it sometimes. Each nasal bone with deep notch anteriorly. Depression on lacrimal fairly large but shallow. Bulla small, rounded, with a fairly smooth surface. Auditory meatus short and without longitudinal crest.

Upper canines absent and even their alveoli closed. Lower incisors and canines with large compressed crowns, asymmetrical, and extremely diverse in size; middle teeth somewhat larger than outer
677 ones. In middle teeth outer portion of crown larger than inner one; in other teeth whole of crown more or less curved outward. Cheek teeth with low crowns (brachyodont) and comparatively broad; ridges weakly seen on inner surface inside lower molars. Dental formula:

$$\mathrm{i}\,\frac{0}{3},\ \mathrm{c}\,\frac{0}{1},\ \mathrm{pm}\,\frac{3}{3},\ \mathrm{m}\,\frac{3}{3} = 32.$$

Dimensions of adult males: Body length about 140 cm; height at shoulders 90 cm or slightly more (but not more than 100 cm); weight up to 125 kg, with an average of 90 kg; maximum skull length 260 to 290 mm. Females are slightly smaller and lighter than males. (V.H.)

Taxonomy

Within the genus *Cervus,* the species under description is sharply isolated and more strongly distinguished than some others. In particular, it is the only representative of the genus in which the antlers develop a palmate portion. Fallow deer were earlier considered by many authors, and even now continue to be so considered by some, a separate genus. This is rather an exaggeration but there is sufficient justification to consider them a special subgenus within *Cervus*. Apparently they constitute a less specialized group and are closest to subgenera *Axis* and *Rusa* (Indian sika and sambar).

Paleontological material does not help in an accurate assessment of the status and origin of fallow deer. Some species are known from the Pleistocene, including present-day ones, particularly from central Europe (Germany). Some authors consider giant peat deer (*Megaloceros*) close to fallow deer, while others find nothing common between them. (V.H.)

Geographic Distribution

The original distribution of fallow deer has undergone radical changes, far greater than in the case of most other deer. The geographic distribution has been distorted on the one hand by the extinction of the species throughout most of its original range, and on the other as a result of its extensive acclimatization.

The process of extinction commenced long ago, at the dawn of human civilization. Contrarily, the animal's introduction into new areas and subsequent acclimatization have taken place only in the last 2,000 years, since the time of the Roman Empire. Consequently, it is extremely difficult to reconstruct the distribution of the species.[3]

The natural range of fallow deer covers southern Europe to the south of the alpine arc, i.e., Pyrenees evidently, southern France, Apennine Peninsula, and the Balkans (in Bosnia the remains of fallow deer are known from pile excavations), and possibly Sardinia and Rhodes. In Africa the range encompasses northwest Africa and
678 also apparently Egypt. It is possible that fallow deer were acclimat-

---

[3] The number of fairly definite references to the former range of the species is very small and most writers confine themselves to stating that the geographic distribution covered the "Mediterranean countries of southern Europe". There are also several contradictions. Thus, there are references in some places to the "Tunisian forest" as a habitation of wild fallow deer and their "true place of origin North Africa, and generally countries around the Mediterranean Sea." More recent writers (Heim de Balzac, 1936) do not, however, recognize this species as occurring in North Africa, even as a fossil, or report its extreme rarity in Algiers and Tunisia, and that too as an acclimatized animal (Allen, 1939). There are references to the occurrence of wild fallow deer currently in Spanish forests; the species is totally excluded simultaneously from lists of wild mammalian fauna of Europe, etc. The reference cited here only represents an attempt at compiling more realistic definite reports.

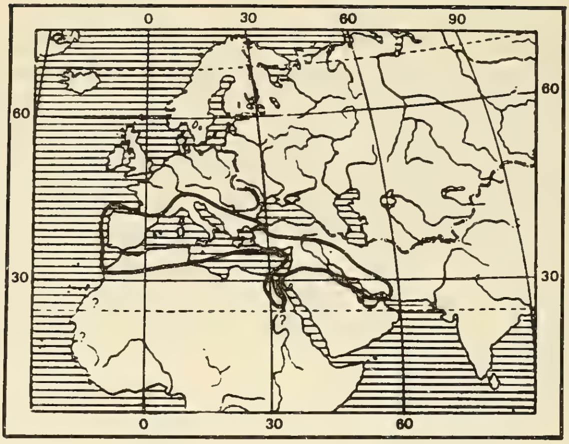


Fig. 231. Probable natural distribution of fallow deer, *Cervus dama* L. in the past. Question marks indicate extremely dubious reports of occurrence in Rio-de-Oro, Senegal-Gambia, and upper Egypt. V.G. Heptner.

ized in Egypt even at the dawn of Egyptian civilization.[4] In Asia the range includes Asia Minor (probably the southern half), Syria. Palestine, Iraq, west and southwest Iran, and Mesopotamia. Fallow deer did not occur, apparently, in the distant past in Trans-Caucasus.

Within this natural range fallow deer have become extinct almost everywhere, or almost so. At several places where they have survived, the animal has been secondarily acclimatized. This is the situation in North Africa, Spain (see footnote No. 3 above), Italy, and some other places. In Iran and Iraq fallow deer survived up to the early part of the present century (lone animals probably still survive); it is possible that fallow deer still survive here and there in the hilly forests of the southern half of Asia Minor, but there is no reliable information about this (see "Geographic Variation"). References are available on the occurrence of fallow deer (*C. d. mesopotamica*) in the Jordan valley even in the 1920's (J. Aharoni, 1930).

Throughout Europe, outside the above line, i.e., north of the Alps, fallow deer are dispersed very extensively in hunting grounds and parks; this artificial range is not inferior to, or only slightly so, the large natural range. Fallow deer are presently raised in Ireland, Scotland, southern Sweden, the far western regions of the USSR (see below), Rumania, Bulgaria, Italy (except Sicily), Sardinia, Spain, Portugal, and throughout central and western Europe.

---

[4] Data on the occurrence of fallow deer in Egypt are based on ancient paintings and are highly contradictory (Hilzheimer, 1926 and 1928). The description of present-day *Dama schaeferi* Hilzheimer from Egypt is apparently based on some misunderstanding. Contemporary authors do not take this form into consideration.

Outside Europe fallow deer have been acclimatized in New Zealand (northern and southern islands) and the Americas. In South America fallow deer are raised north of Valdivia in Chile and at several places in Argentina. In North America they have been colonized in western Nebraska and Kentucky (USA).

Within the Soviet Union fallow deer were never widely distributed although they have lived here for quite a long period. Even during the sixteenth century animals survived in the forests of Lithuania and Belorussia and in the early eighteenth century in Belovezh Forest (Kirikov, 1952; Serzhanin, 1955). These, however, were important animals even though there are no direct references to
679 the import of fallow deer into Belovezh Forest before 1860 (Kartsov, 1903). Toward the end of the last and the early part of the present century, there were only a few small habitats of fallow deer in the extreme west of Russia in some game farms, of which Belovezh Forest was the most important. These animals were all destroyed by 1920. From 1880–1890 and 1917–1920 fallow deer survived around Borzhomi (Borzhomi animal *otvod* [distribution center]) in Georgia.

At present (mid-1950's) fallow deer occur in only five areas in the USSR: Volozhinsk and Ivanets regions of Molodechnensk district where the animals were imported from Germany in 1932 (Serzhanin,

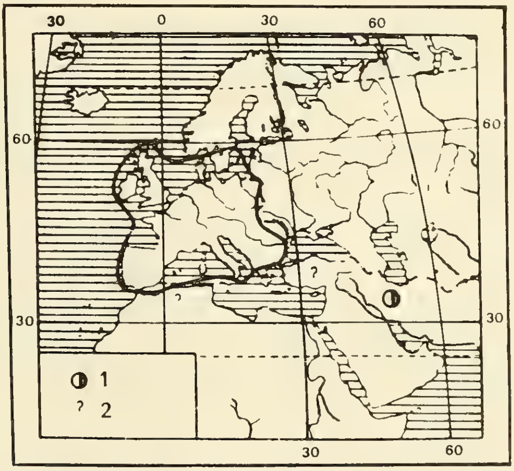


Fig. 232. Present-day distribution of fallow deer, *Cervus dama* L., in the Old World.

1—distribution of Mesopotamian fallow deer, *Cervus dama mesopotamica* Brook, in Iran; 2—probable distribution of fallow deer but adequate information not available. V.G. Heptner.

1955); western part of Lithuanian Republic where the animals were imported in the 1890's (Kuznetsov, 1954); Askaniya-Nova; Khortits Island on the Dnieper near Zaporozh'ya (Korneev, 1952); and Biryuchii Island in the Sea of Azov (Azovo-Sivash preserve).

The population of fallow deer is small everywhere and evidently not more than 200 animals are present in the USSR.[5] (V.H.)

Geographic Variation

Two subspecies occur in the species.

1. Common fallow deer, *C.* (*D.*) *d. dama* Linnaeus, 1758.

The characteristics of this subspecies have been described above.

This subspecies occupies the entire present-day range in Europe. In the past it apparently was present over much of the natural range in addition to the small areas populated by the second subspecies described below. This nearly nominal form occurred throughout its natural range and was wholly monotypic. It is probable that the populations of the Asia Minor and northwest African races differed. However, no evidence whatsoever is available in support of this assumption. At present, throughout its artificial distribution, animals in different regions tend to differ (size, color, frequency and diversity of color mutations, and so on)—the result of human intervention and not natural geographic variability.

2. Iranian fallow deer, *C.* (*D.*) *d. mesopotamica* Brooks, 1875.

In size this subspecies is somewhat greater than the preceding one, brighter in coloration, and the antlers without a palmate portion, or with only a very insignificant enlargement of the terminal portion.

The natural range of this form extended from Syria and Palestine through Iraq and Mesopotamia into southern and southwestern Iran. It is possible that in the remote past (even in the predynastic period), this subspecies, or some other subspecies closely resembling it (Hilzheimer,1926 and 1928), survived in Egypt (some regard it as acclimatized there). In the last century the range was confined to the forest regions of southwestern Iran (Luristan, Zagros, and Kermanshah) and adjoining parts of Iraq. In this region the range of fallow deer steadily declined but the animals survived until the early twentieth centery. By 1920, however, they were practically extinct. The last recorded capture occurred in 1917 (Ellerman and Morrison-Scott,

---

[5] Further acclimatization of fallow deer within the USSR is not of particular interest since sika, far more valuable in scientific, aesthetic, and practical contexts, are already available here. (V.H.)

680 1951). Some stray individuals might still be surviving in the hilly forests of the Iraq-Iran border.[6]

This form used to be considered an independent species. Some authors hold this view even now. Both forms are undoubtedly very closely related and their ranges in the past were evidently continuous and vicariant [parapatric].

Only the nominal form has been used for purposes of acclimatization. (V.H.)

Biology

Population. Breeding fallow deer in parks was very popular in the Pri-Baltics in the nineteenth century. Nevertheless, they remained very few in numbers since they withstand severe winters with difficulty. Commencing from 1860 fallow deer were imported into Belovezh Forest several times.[7] Generally numbering several dozens, the animals were obtained from Poland, Czechoslovakia, Pri-Baltics, and other places. They were originally held in pens and only a small number set free. In 1899 all fallow deer were released in the forest and turned feral. In this forest 740 fallow deer were counted in 1901, 750 in 1905, 1,250 in 1907, 1,209 in 1908, and in 1914 up to 2,000 (Wroblewski, 1927). During the years of World War I those Forest deer were destroyed and by 1920 none remained. A small population in Gatchina Game Farm near Petersburg escaped slaughter.

From 1888 to 1890, 120 fallow deer were imported from different regions (Hungary, Pri-Baltics, and others) into Borzhomi Game Park (the so-called Borzhomi otved) in Trans-Caucasus and released in a large pen. The animals multiplied well (Anonim, 1891) but disappeared in this region soon after 1917. A small number of deer were also held in private parks, pens, etc. in the Ukraine (for example, in Askaniya-Nova and Pri-Carpathians) and at places farther north. They disappeared almost everywhere after 1917.

At present the maximum number of fallow deer in the Soviet Union is found in the Pri-Baltics. About 100 were counted in the Lithuanian Soviet Socialist Republic in the early 1950's, 120 in 1955, and 137 in 1957 (Kuznetsov, 1952; F.L. Ivanauskas; and others). A small number live in Askaniya-Nova from where they were exported to Azovo-Sivash preserve on Biryuchii Island in the 1940's and numbered 15 in 1958. Ten fallow deer from Askaniya-Nova were sent to "Sukholesy" protected area in Kiev district in 1952 and are flourishing. Five deer were found in 1947 in the territory of Vyalov protected area[8] (Volozhin and Ivanets regions of Belorussian Soviet Socialist Republic) (Serzhanin, 1955).

---

[6] In 1957 and 1958 a small number of Persian fallow deer were unexpectedly found in Arabia in the region of Karun, Dez, and Karshekh Rivers, living in tugai (Haltenorth, 1958 and 1959). A thorough revision of this form led Haltenorth to conclude that it is an independent species. However, it is very close to European fallow deer.

[7] Until then fallow deer had time and again been found living freely in the Forest, having penetrated there from adjoining private estates. In the early eighteenth century they were not rare in this region (Kirikov, 1952).

Habitat. The most suitable habitats of fallow deer are plains and slightly rugged or hummocky locales where small deciduous forests alternate with grassy clearances and shrubs. Fallow deer often visit forest edges, especially in summer, and sections in which shrubby undergrowth is well developed, primarily in winter. In Belorussia fallow deer inhabit dry spruce-pine plantations with a dense undergrowth and good grass cover. Juveniles are particularly fond of shrubby patches with dry meadows nearby. In summer they often graze in forest clearings, cut-over sections, and in dry meadows (Serzhanin, 1955); in winter they graze in forest areas rich in underbrush and saplings including pine.

Food. In summer fallow deer feed on grassy vegetation and avidly eat leaves and very thin shoots of deciduous trees. Among 681 browse foods, the most important are the bark and branches of pine, willow, hornbeam, aspen, oak, mountain ash, maple, and other species. In winter and spring they nibble shoots of needles and the tops of young pine and gnaw the bark of much larger saplings. In their preference for arboreal foods fallow deer lag slightly behind red deer but outstrip roe deer. In West Germany fallow deer greatly damage willow, oak, ash, and hornbeam and less so beech, maple, fir, pine, and other species (Ickermann, 1956). Fallow deer also consume acorns, nuts, and probably beechnuts. In winter they eat standing dead vegetation, fallen leaves (as long as they are not shriveled), and arboreal lichens. In Belorussia in summer they consume grasses, sedges, umbellifers, and legumes. The intake of anemones, *Corydalis,* squills, and the shoots of deciduous trees and pine has been observed in early spring. In autumn they are fond of visiting oak groves for fallen acorns. In winter they consume heather, whortleberry stalks, and the bark of aspen, pine, and even spruce (Serzhanin, 1955).

Fallow deer quite often visit artificial salt licks; they use them best in spring and in the first half of summer.

Home range. The territorial behavior of fallow deer in the Soviet Union has not been studied. Fallow deer, more than red deer, are confined to a given section of the habitation within which they spend most of their life.

---

[8] Fallow deer had been imported there in 1932 from Germany and Austria. In 1937 they numbered 48 and in 1940 only 33 (Serzhanin, 1955).

Daily activity and behavior. In summer grazing and rest alternate throughout the day. However, in warmer hours the animals usually lie down or stand in dense shrubs warding off blood-sucking insects; grazing animals are maximum in morning and evening hours. During dry summers fallow deer regularly visit water holes and salt licks, forming beaten trails to them. Fallow deer are less adapted to movement through deep snow because of their short legs and heavy body weight. Their olfactory and auditory senses are highly developed but vision is also considered quite good.

In summer adult females with young move singly or in small groups, forming larger herds by August. Males in the warm period of the year live singly or in small groups. In winter, primarily at its commencement, mixed herds are sometimes encountered, but males and females usually move separately. The herding instinct is more pronounced in winter than in summer.

Within the Soviet Union fallow deer undertake only minor migrations from one area to another.

Reproduction. Fallow deer come into rut at a much later period than red deer. In Belorussia rut commences in the last ten days of September and ceases at the end of October; estrus peaks around October 10 to 20 (Serzhanin, 1955). In Soviet zoological gardens the period of estrus extends from the end of September through October inclusively (Flerov, 1952). During rut an adult male joins a herd of females. Juveniles moving with the herd of females are chased away. Fawns born in the summer of that year usually remove themselves when the male in rut joins the herd, rejoining their mothers later.

During the period of rut adult males emit spaced hoarse calls throughout the night, more often in the evening and at dawn. Combats between males over females are often vicious. Males in rut are irritable and lose their normal caution. Only males aged four or five years mate since younger animals (males attain sexual maturity at the age of 1.5 years) cannot successfully compete with older rivals. Some females mate in their second year and some in their third.

Gestation lasts 7.5 to 8.0 months. Parturition of fallow deer in Belorussia occurs in June (Serzhanin, 1955). Usually a single fawn is born (especially in the case of younger females) and rarely twins. Before giving birth the female leaves the herd. In the Federal Republic of Germany parturition of fallow deer commences from the latter half of May. Only 12% of gestating deer fawn in May, 72% in June, and 16% in July (Rikk; cited from Ickermann, 1956).

682 *Growth, development, and molt.* Fawns are helpless during the first few hours of their birth but can even run by the second day. They usually remain, however, at the site of their birth for several days with the mother grazing close by. At the age of one week or

somewhat later fawns start to follow their mothers. Lactation continues up to the next period of estrus or somewhat longer, almost until spring in some females. Fawns begin feeding on grass in their fourth week (Turkin and Satunin, 1902). They follow their mother at least until next fawn is born.

At about six months of age male fawns sport knobs and unbranched antlers, generally in the second half of February to March. Antler growth ceases by the middle of April. They are tender and very sensitive to impact and mosquito bites. The antlers gradually ossify and by the end of July to August, i.e., at the beginning of their second year, males rub the velvet off against branches of small trees. The first antlers of fallow deer are shed at the end of the second year, from mid-April through May. Between May and June new antlers commence growth which bifurcate. Velvet is rubbed off from mid-August to mid-September and the antlers shed in the following year from mid-April through May. In each successive year the antlers are more complex, attaining maximum growth when the animal is five years old or older. In older fallow deer antler deterioration is discernible (Ickermann, 1956; and others).

In West Germany antler growth in adult fallow deer occurs in May to June, velvet is discarded in August to early September, and antlers are shed in April (Ickermann, 1956). In the Soviet Union calendar periods of antler growth have not been thoroughly studied and the process of molt has yet to be traced.

The life span of fallow deer is 20 to 24 years (Severtsov, 1940); some survive up to 33 years (Ickermann, 1956).

Enemies, diseases, parasites, mortality, competitors, and population dynamics. Wolves inflict utmost damage on populations of fallow deer. Lynx sometimes attack them but occur in small numbers in regions of fallow deer occurrence and hence are not serious enemies. Foxes and wildcats [*Felis sylvestris*] pose a danger for newborn fawns.

Fallow deer are poorly adapted to snowy winters; mortality invariably increases in the herds at this time (Pri-Baltics and Belovezh Forest). During continuous snow on Biryuchii Island in the severe winter of 1953 to 1954 a large number of red deer died and mortalities among fallow deer were also reported (Ishunin, 1956).

The diseases and parasites affecting fallow deer in the Soviet Union have almost not been studied. Cases are known of Siberian ulcers, hydrophobia, leptospirosis (Czechoslovakia), and distomatosis (Ickermann, 1956; and others). Instances of fallow deer being attacked by itch mite *Acarus siro* (Dubinin, 1955) have been recorded in zoological gardens. The larvae of the gadfly *Paryngomyia picta* are known to parasitize the nasopharynx of fallow deer (Grunin, 1957).

The most serious competitor of fallow deer is red deer (Wroblewski, 1927) and to a lesser extent roe deer and moose (the latter occur in small numbers within regions in the Soviet Union where fallow deer are resident).

Some idea of the population structure of fallow deer may be had from census data recorded in Belovezh Forest. In March, 1909 there were 1,209 fallow deer, of which 1,026 were adult animals and 183 fawns (about 15% of the entire population) (Wroblewski, 1927). Fawns represent 42% of all females aged 1.5 years and older.

For normal reproduction of the herd a single male suffices for five or six females. In Belovezh Forest, however, males are numerous and competition for females brisk.

Field characteristics. Fallow deer are smaller in size than red deer but perceptibly larger than European roe deer. The height at withers is slightly less than a meter. The general summer color is bright rusty with large white spots on the upper side of the body. In winter the coat is darker and the spots very faint. The horns are large,
683 branched, with a large palmate portion at the end and tines at the rear. Females have no horns but resemble males in other external features.

Hoofprints of adult fallow deer are only slightly larger than those of a five-month-old red deer, but are more elongated and strongly pointed toward the front. The tracks are also similar to those of sheep but the front ends of sheep hooves are blunter and more wideset. Hoofprints of males are larger than those of females.

Feces are somewhat smaller than those of red deer. (A.N.)

Economic Importance

Before the Great October Revolution fallow deer served as an object of hunting for the privileged classes of Russian society and were specially raised for this purpose (Belovezh Forest, Gatchina Game Farm, Borzhomi Game Farm and so on). Most often, hunting was done with beaters, more rarely with the help of dogs, by ambush, or "still-hunting".

The meat of fallow deer is tougher than that of red deer but tasty; it contains more fat in autumn. The meat of males in the period of rut is almost unsuitable for consumption. The body weight of large males may reach 90 to 100 kg while females weigh less. The hide is suitable for making high-quality thin chamois (it is more expensive than the chamois made from the skin of red deer).

Antlers are used as wall decorations.

In western Europe where fallow deer are abundant, they damage forest plantations. In magnitude this damage is considered no less important than that caused by red deer in some cases. The damage caused by fallow deer in Belovezh Forest is estimated to be of a similar magnitude (Kartsov, 1903; Wroblewski, 1927). In the Vyalov protected area fallow deer damage pine by breaking the tops of young trees (Serzhanin, 1955).

Fallow deer are extremely few in numbers in the Soviet Union and are protected everywhere. (A.N.)

PART II

ORDER OF ODD-TOED UNGULATES

Order PERISSODACTYLA Owen, 1884

Superorder MESAXONIA Marsh, 1884

Order PERISSODACTYLA Owen, 1848

687 Perissodactyla comprises a highly specialized order of land mammals and includes species of large size, and light and slender or heavy build.

The number of digits on the forelimbs is four (I absent), three (I and V absent), or one (only III present), and on the hind limbs three (I and V absent) or one (only III present). The remaining metapodial elements are correspondingly reduced or rudimentary. Rudiments of digits II and IV are seen in monodactyl forms (splint-bones). The limb axis invariably traverses through the third digit (mesaxonal). If there are several digits, III is developed more intensely than the rest and the lateral digits are smaller than the medial ones (V is sometimes large), but so arranged as to lie in a single plane and not otherwise. The bones of digit III are axial. The terminal phalanges are covered with hooves in the shape of an enlarged nail, or a horny cover of a circular shape encompasses the terminal phalanx (in monodactyl species). The hoof of the middle digit is invariably symmetrical and usually larger than the rest. Asymmetry in the lateral digits is usually very slight. In multidactyl species all digits have a common sole pad.

In some forms, as a result of adaptation to fast running, all parts of the limbs (except the proximal) are greatly elongated, while in other forms they are relatively short but also highly specialized for fairly fast movement. Pronation and supination are absent and the limb is capable of flexure only in the sagittal plane. Collar bone absent. Third trochanter of femur present. Ulna and fibula in some forms developed normally and independent, while in others they are reduced to some extent and fuse with the radius and tibia. Astragalus with a single (proximal) articular surface.

There are 22 or 23 lumbar-thoracic vertebrae. Skeleton of tail greatly reduced.

As a result of elongation of teeth and the dental row, the skull of some forms has a greatly elongated facial portion; in other forms with a somewhat shorter dental row the length of the facial portion almost equals that of the cranial portion. Skull usually highly pneumatized. Orbit confluent in some, but separated (from temporal fossa) in others. Ethmoid pit absent. Alisphenoid canal invariably present. Nasal bones enlarged posteriorly. In some species one or 688 two, sometimes large, "horns" in the form of an overgrowth of epidermis occur in the nasal and frontal regions in the sagittal plane.[1] Base of horn without bony or horny core.

Teeth heterodont and diphyodont. Complete dental formula:

$$i\frac{3}{3},\ c\frac{1}{1},\ pm\frac{4}{4},\ m\frac{3}{3} = 44,$$

but usually dentition is somewhat reduced from

$$i\frac{3}{3},\ c\frac{1}{1},\ pm\frac{4}{3},\ m\frac{3}{3} = 42 \text{ (tapir) to}$$

$$i\frac{0}{0},\ c\frac{0}{0},\ pm\frac{3}{3},\ m\frac{3}{3} = 24 \text{ (white rhinoceros).}$$

Diastema present. Molars with ridges (lophodont) or crescentic ridges (selenolophodont) with complex enamel patterns, brachyodont or hypsodont.

Stomach simple, cecum large, and gall bladder absent. Complex skin glands absent. Pelage consists of normal, short, close-growing hair, sometimes greatly elongated at places (mane on neck and tassel on tail); in some animals hair cover greatly reduced or almost absent. Teats two and inguinal. Scrotum well developed, inguinal; in some animals testes subcutaneous. Uterus bifid. Placenta diffuse. Sexual dimorphism absent or weakly expressed; age-related dimorphism sharp in some species (tapir), and absent in others; seasonal dimorphism evident in a few forms.

In build, outward appearance, and to some extent size, perissodactyls do not vary as much as artiodactyls. The group comprises three forms—rhinoceros, tapir, and horse. The largest of these (white rhinoceros, *Diceros simus*) has a body length of 400 cm, stands up to 180 cm at the withers (at nape of neck up to 215 cm) and weighs up to 2,000 kg[2]; the smallest (Asiatic tapir, *Tapirus indicus*) has a body length of about 200 cm, stands about 100 cm at the withers, and weighs up to 235 kg.[3]

Some forms of perissodactyls (horse) exhibit a high degree of specialization of the "hoof," far greater than in artiodactyls. At the same time, this represents one of the extreme levels of specialization among mammals as a whole.

---

[1] The known maximum length of a horn, measured along the curvature, is 1,556 mm (*Diceros s. simus* Rode, 1944).

[2] Some specimens of Indian rhinoceros (*Rhinoceros unicornis*) are apparently somewhat larger.

[3] Some forms (African ass, *Equus africanus*) weigh less although their linear dimensions (height at withers) are somewhat greater than in smaller forms of tapirs.

Some species are fleet-footed, slender, and stand on long legs; others are heavy in build, massive, and with short legs. The group occupies chiefly open expanses such as deserts, steppes, forest-steppes, but in part wet and swampy tropical forests, and at places foothills, uplands, and open places among mountain clearings.

Perissodactyls are mainly solitary animals but some live in small groups and more rarely form herds. Most are resident animals but some perform fairly regular seasonal migrations. They are polygamous and give birth to a single calf, born in a highly developed state and capable of running immediately after birth. Males do not participate in the care of offspring.

These are strictly herbivorous animals feeding mostly on grasses; a few feed on shrubs and aquatic plants.

Perissodactyls are widely distributed but their distribution is more restricted than that of artiodactyls. These are predominantly Old World species with a rather restricted distribution in the New World. They are absent in Australia and Madagascar. The range of the order covers all of southern Africa, in the west northward approximately to 10° S lat. (southern boundary of west African forests), and in eastern Africa on the west up to the eastern edge of west African forests (encompassing the southeastern, easternmost, and northeastern parts of the Congo, i.e., in the west roughly to 27 to 28° E long.), in the east to the seacoast, Ethiopia, Somali, and
690 Eritrea, Sudan Republic, except northwestern parts, Ubangi-Shar, southeast of Lake Chad, much of Cameroon, and northeastern parts of Nigeria (southwest of Chad). Thus the range surrounds the tropical forests of western Africa from the south, east, and north. In the north the distribution of perissodactyls covers the Egyptian region of the United Arab Republic and northwestern Africa. Perissodactyls are evidently absent in the Sahara and Libyan deserts and regions adjoining the Gulf of Guinea.[4]

In Eurasia the range covers the Arabian Peninsula, Asia Minor, Syrian region of the United Arab Republic, Palestine, Iraq, Iran, eastern Trans-Caucasus, Afghanistan, India (absent in Sri Lanka), Indochina Peninsula, Malacca, Java, Sumatra, Kalimantan (Borneo), Tibet (including Ladakh), Kashgar, Dzhungaria, Inner Mongolia, Mongolian Republic, western regions of northeastern China, and southeastern Trans-Baikal. Farther in the west the range (reconstructed) covers the forest-steppe, steppe, and deserts of western Sibe-

---

[4] See the characteristics of horse family.

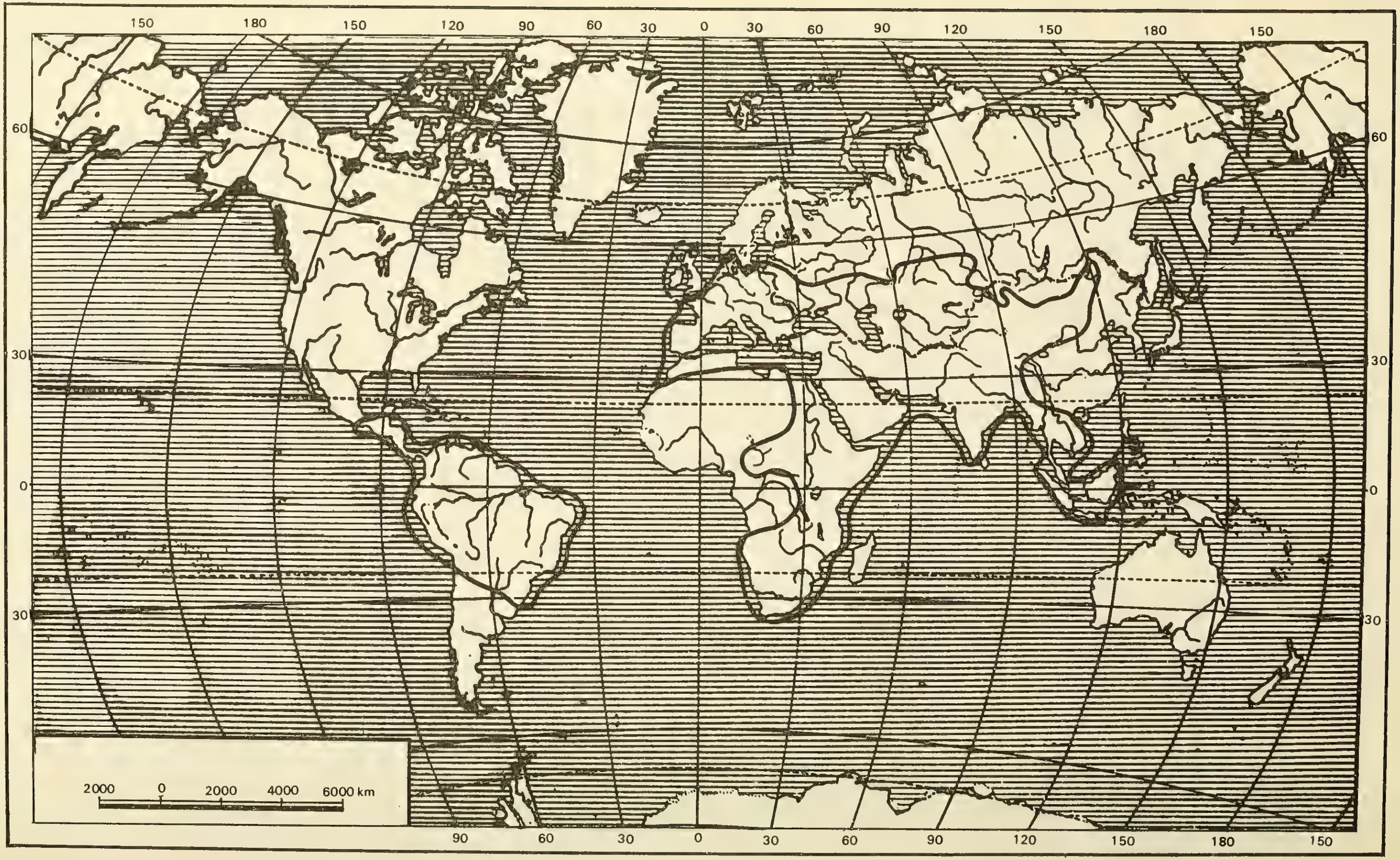

150
180
150
120
90
60
30
0
30
60
90
120
150
180
150
60
30
0
30
2000
0
2000
4000
6000 km

Fig. 233. Reconstructed distribution of order Perissodactyla (scale in km). V.G. Heptner.

ria, Kazakhstan, Middle Asia, eastern and central Europe, and part of the forest regions of central, western, and eastern Europe.[5] The animals have presently disappeared from much of their range (wholly in Europe and over much of Asia).

In the New World the range includes South America north of a line running from northern Chile to the lower courses of the Parana and Uruguay [rivers], and Central America including southernmost Mexico (except northern Yucatan).

Because of their small number of biological types, fewer species, and restricted distribution, one cannot compare them with artiodactyls. They represent a group which has passed the peak of evolutionary development. The rapid extinction of some species and the undoubted threat of rapid extinction of the remaining ones is exclusively associated with human intervention in all its manifestations, but mostly through direct killing. Nevertheless, perissodactyls cannot be termed a dying group.

In their affinities perissodactyls usually are placed with artiodactyls; sometimes the former are even considered a suborder of the single order of ungulates. In fact, these two are extremely isolated groups; their similarities are mainly explained by convergence (see characteristics of order Artiodactyla).

In origin perissodactyls (like artiodactyls) are related to [ancestral] primitive carnivores (Creodonta). True perissodactyls appeared in the Lower Eocene. During this period present-day forms such as Equidae (horse) and Tapiridae (tapir) were also present together with already extinct families (Palaeotheriidae, Brontotheriidae, Titanotheriidae, Isectolophidae, Lophiodontidae, Chalicotheridae; and others), while Rhinocerotidae (rhinoceros) appeared somewhat later (Middle Eocene). In fact, these forms are still quite far removed from recent ones[6] but the course of their development is distinctly discernible.

All groups of the order (also those which later became extinct) developed very rapidly and became the dominant forms of ungulates, suppressing other groups, especially certain artiodactyls, by numbers and partly by diversity. By the Miocene perissodactyls began to lose their importance (some groups became wholly extinct even in the Oligocene) and gave place to some rapidly flourishing artiodactyls. Rhinoceros and horse were still relatively abundant in the Upper Tertiary (Pliocene) and partly even in the Pleistocene.

[5] See following description of distribution of onager and tarpan.

[6] *Hyracotherium* (*Eohippus*) from the Lower Eocene of North America possessed four digits on the forefeet and three on the hind, and was the size of a fox terrier.

Nevertheless, the order suffered a sharp decline in the Pliocene.

In the past not only was the diversity and number of species far greater but also the distribution was wider, covering all of North America and northern Asia where perissodactyls lived even in the Pleistocene. North America represented the region in which a significant part of the history and evolution of the order took place.

691 The classification of perissodactyls is comparatively quite simple due to the fewer number of forms and the sharp morphological differentiation of the groups comprising the order. There are no significant controversies. Two suborders are usually recognized—Hippomorpha and Ceratomorpha—comprising three families: in the Hippomorpha—Equidae (horse), and in Ceratomorpha—Tapiridae (tapir) and Rhinocerotidae (rhinoceros). Sometimes three suborders are recognized, corresponding to these three families, or the order is not divided into suborders but simply into families. Controversies concern only this aspect. There is no controversy over the number and size of families.

All the fossil groups are likewise included in the suborders indicated above. Fossil material on perissodactyls is very extensive and many studies have been devoted to this group; thus it is one group of mammals whose paleontological history has been thoroughly studied. Very reliable paleontological phylogenetic series have been worked out for some perissodactyls (horses, titanotheres).

The order contains 153 genera and 12 families, of which 9 are extinct; extinct genera number 147 and modern, 5. Of the latter, one genus comprises horses, three of rhinoceros, and one genus of tapir.[7]

The number of species of present-day perissodactyls (including species extinct in historic times) is 15. These are: six species of horse (genus *Equus*), two species of African rhinoceros (broad-muzzled* or black *Diceros bicornis* Linn., 1758 and narrow-muzzled* or white *D. simus* Burch., 1817), three species of Asiatic rhinoceros (Sumatran, *Didermoceros sumatrensis* Fish., 1815; Javan, *Rhinoceros sondaicus* Desm., 1822; and Indian, *Rhinoceros unicornis* Linn., 1758), and four species of tapir (Indian, *Tapirus indicus* Desm., 1819; and American—common, *T. terrestris* Linn., 1766; mountain, *T. pin-*

---

[7] Attempts have been made time and again to further split the group but none was well founded.

To judge the degree of modernization it is important to note that only about 4.0% of all genera of perissodactyls have survived until now, versus about 26% in the case of artiodactyls. The number of present-day species of perissodactyls constitutes about 8.0% of those of artiodactyls.

*This appears to be a *lapsus* in the Russian text; *D. bicornis* is the black or hook-lipped rhino, while *D. simus* is the white or square-lipped rhino—Sci. Ed.

chaque Roul., 1829; and Baird's, *T. bairdi* Gill, 1865). These represent about 0.3% of all mammals. On the average, each genus contains three species and each family five. Most of the species occur in Africa (six—four species of horse and two of rhinoceros) and Asia (six—two species of horse, three of rhinoceros, and one tapir); only three species (tapirs) occur in the Americas.

Perissodactyls represent a group of game animals providing meat, hide, and raw material for the Chinese pharmacopoeia[8] or serve as game animals. In the past, often even in recent times, they were highly valued as objects of hunting in some areas. However, at present this has no relevance since the population of all the species has declined drastically and, in spite of some efforts to arrest it, has continued to decline. Some species and races have become totally extinct. Such are the southern Russian tarpan, some forms of onager, two forms of quagga (*Equus q. quagga* and *E. q. burchelli*), and wild ass (some animals have survived in zoological gardens). Several races and species are on the brink of extinction, namely, the true zebra (there are less than a hundred *E. z. zebra*), Javan and Sumatran rhinoceros (less than a hundred combined), Indian rhinoceros (about 400 in all sanctuaries), and the Central Asiatic wild horse (Przewalski's horse). For the reasons stated above all these species are protected under conservation laws to some extent, some are totally protected, and some preserved only in sanctuaries. In most cases, conservation measures have not succeeded and populations of all species are falling rapidly.

Perissodactyls have given rise to two important domestic animals, the horse and the ass. The parent stock of the former was the tarpan (*E. przevalskii*) and that of the latter, the African wild ass (*E.*
692 *africanus*). These species are thus found in both wild and domestic states. Attempts at domestication of kulan (*E. hemionus*), undertaken recently in the USSR, have not yielded satisfactory results. Yet some instances of utilization of kulan as domestic animals are known in recent times as well as in the distant past. Older writers mention the use of kulan ["onagers"] as draft animals. It has also been suggested that the kulan was domesticated in Mesopotamia before the horse was. Kulan do not represent the parent stock from which present-day domestic ass evolved, although it has been suggested that strains of tall asses of certain regions in eastern Iran were

---

[8] The blood and especially the horns of rhinoceros are greatly valued in the Chinese and Malayan system of medicine. The value of these horns offsets all the efforts, difficulties, and risks involved in catching the animals, and has been primarily responsible for their extinction not only in Asia, but partly also in Africa. Moreover, almost all the body parts of rhinoceros are used for medicinal purposes.

formed as a result of the admixture of the blood of kulan. The suggestion of some, especially older writers, about the contribution of the kulan to the evolution of domestic horse cannot be justified. Attempts at domestication of zebras (at one time quite numerous) did not yield desired results and were abandoned.[9]

Acclimatization of perissodactyls on a significant scale has yet to be attempted.

The fauna of the Soviet Union includes (counting also the extinct tarpan) two species[10] (about 13% of the species of the order and about 0.6% of mammalian species of the USSR). One of the two suborders, one of the three families, and one of the five genera are represented in the Soviet Union.

The range of perissodactyls (reconstructed) in the Soviet Union encompasses forest-steppe, steppe, and desert zones, and in part the region of western broad-leaved forests.

Perissodactyls are gregarious animals and live in groups. Seasonal migrations are undertaken. They are polygamous animals and molt twice a year. Sex-related and age-related dimorphism are absent.

Perissodactyls in the Soviet Union are presently of no economic importance, in fact they are protected. In the past they constituted hunting and game animals. (V.H.)

---

[9] The purpose of these and similar attempts with respect to eland (*Taurotragus*) was to produce a transport animal immune to trypanosomiasis, which is responsible for the death of European domestic animals in most parts of Africa.

[10] Assumptions about the occurrence of some rhinoceros-like animal on the Volga in the historic period (tenth century) should not be considered proved. They are based on a description by Ibn Phadlan, a most confused and even fantastic account, which contains characteristics having nothing in common with rhinoceros ("head like that of a fleeced lamb," "body like that of a mule," and so on). However, according to some authors the description leaves no doubt (Pidoplichko, 1951) that Ibn Phadlan did have the rhinoceros in mind. The best course would be to discard this report as yet another of the fantastic accounts which abound in journals kept by even the most conscientious of ancient travelers in the Middle Ages. Ibn Phadlan's extraordinary "animal" was the result no doubt of his confusing information about moose, which at that time (at places even now) lived in forest-steppes, with reports on rhinoceros.

Suborder of Horses

693 Suborder HIPPOMORPHA Wood, 1937

Superfamily EQUOIDEA Hay, 1902[1]

Family EQUIDAE Gray, 1821

Perissodactyls of moderate to very small size, light and slender build, and standing on tall thin legs.

One digit (III) present on fore and hind limbs. Lateral digits represented by rudiments of metapodia (II and IV), seen in the form of "splint-bones". Hoof covering of enlarged and massive terminal phalanx in the form of a circular horny shell. In view of adaptation to fleet-footedness all the segments of the extremities are elongated (except the proximal). Ulna and fibula significantly reduced and often fused with radius and tibia.

Thoracic vertebrae 18 or 19, lumbar vertebrae 5 or 6 and sacral vertebrae 5 or 6.

Facial part of skull highly elongated. Orbit closed from behind. Nasal bones narrow, long, and insignificantly enlarged at base. Premaxilla well developed and massive; nasal processes large, envelop nasal opening from the sides, and join nasal bones. Horns absent.

Dental formula:

$$i\frac{3}{3},\ c\frac{1}{1},\ pm\frac{3}{3},\ m\frac{3}{3} = 40.$$

Sometimes in the upper jaw, more rarely in the lower, there occurs an additional premolar ("wolf tooth") in which case the formula of premolars would then be $pm\frac{4}{3}$ or $pm\frac{4}{4}$ and the total 42 or 44. However, this tooth is usually small and lost early in life.

Cheek teeth hyposodont,[2] squarish in section, seleno-lophodont, and with a very complex enamel pattern; cavities of patterns filled with cement. Enamel pattern of upper premolars no less complex than that of molars ("molarized") and usually slightly larger than them. Masticatory surface of incisors with enameled loops and depressions filled with cement. Canines of males well developed but 694 in females small (not larger than incisors), compressed at sides, and rudimentary or absent. Molars separated from incisors by a prominent diastema. Upper canine roughly at middle of diastema while lower is adjacent to incisors.

---

[1] Includes, in addition to Equidae, extinct Palaeotheriidae.

[2] Extreme stage of hypsodonty. Roots are very small, close late, and the permanent teeth prismatic for some period of the animal's life.

Kidneys nonlobate. Only one vena cava present. Pelage normal, dense, close-fitting, and short. Short, upright mane[3] occurs on neck and tail fairly long with long hair (tuft) at end or all along its length. Color fairly monochromatic, of yellow or gray tones, or entire body or only anterior part striped (blackish-brown bands on light-colored field). Scrotum well developed. Sex-related and age-related dimorphism absent but slight seasonal dimorphism evident in some individuals.

Species of family highly monotypic in general build and differ externally only in size and color, well-known variations among horses. In size large forms correspond to smaller domestic horses (height at withers up to 130 to 150 cm) and smallest correspond to small forms of domestic ass (height at withers 105 to 115 cm).

The horse family represents a very progressive and highly specialized group of perissodactyls and thus a highly specialized group among land mammals.

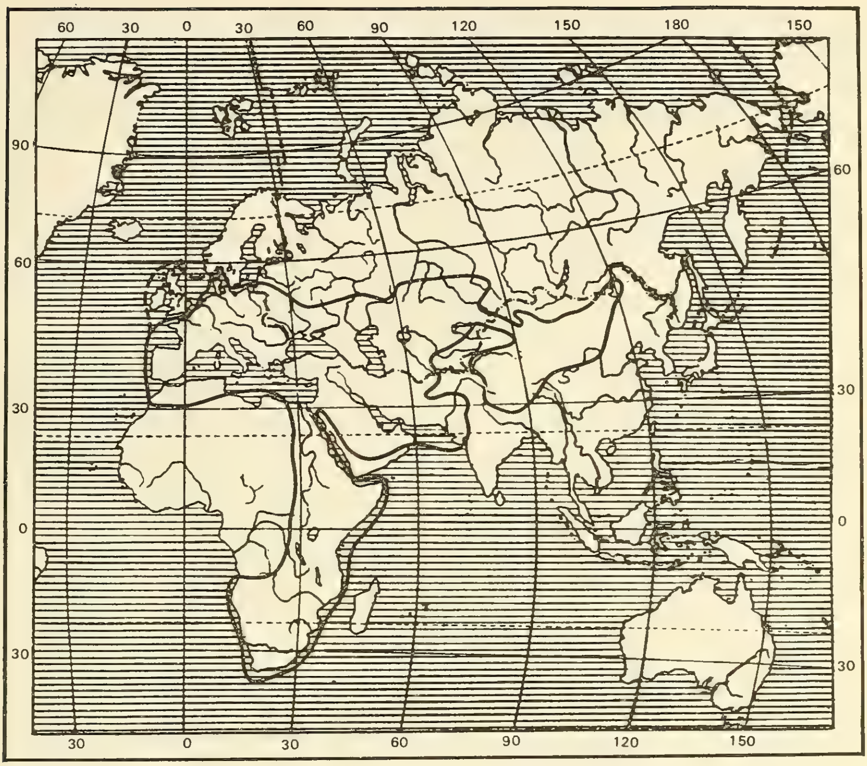
All members of the family are cursorial animals and inhabit steppes, semideserts, deserts, forest-steppes, open montane plateaus 695 and foothills. They avoid forests although some forms once lived in them (probably the result of displacement by man). They live in small herds or troops, some in groups of three to five animals, sometimes (rarely) forming large congregations. Some species exhibit fairly regular migrations. Their food consists of grassy vegetation.

The natural habitat of the family is restricted to the Old World but is fairly extensive. It ranges from the southern part of Africa northward roughly to 10 to 11° S lat., east Africa on the west to the forest regions of the Congo basin and Ubangi-Shar region (absent in the whole of this part of equatorial Africa and elsewhere), and on the east to the coast of the Indian Ocean, Ethiopia, Somalia, and Eritrea, eastern parts of Sudan, Egypt except its westernmost parts, and northwest Africa.[4] In Eurasia the range includes the Arabian Penin-

---

[3] One form (southern Russian tarpan) apparently bore a somewhat longish, slightly falling mane. The latter, like the forelock, is characteristic of domestic horses.

[4] Early and recent (1930's) information about the occurrence of wild ass (*Equus africanus*) in the Sahara (Tibesti region, Ahaggar, and some others) is dubious. It is probably based on observations of domestic animals left behind or discarded by Tuaregs, which later turned feral.



694 Fig 234. Reconstructed distribution of family Equidae and genus *Equus* L. V.G. Heptner.

sula, Iran, Iraq, Baluchistan, northwest India, Afghanistan (except its easternmost part), Tibet (including Ladakh and Nepal), Kashgar, Inner Mongolia and the Mongolian Republic, the western fringes of Manchuria, eastern Trans-Baikaliya, Dzhungaria, Cis-Altai steppe, Barabin steppe, Kazakhstan, and the plains of Middle Asia. In Europe the range in the historic period included the southern Russian steppes (in the north at least to Voronezh), Lithuania, Poland, Germany, and apparently some other regions including Spain (Strabo's reports in the first year of the present era).

At present the range is sharply reduced and the animals have disappeared over much of the area of their former distribution. They survive only in South (except the extreme south) and East Africa, in Ethiopia,[5] Iran, Afghanistan, and Baluchistan, and probably still survive at some places in northwest India, Tibet, Mongolia, Dzhungaria, and southern Turkmenia.

---

[5] In Somali, Eritrea, and Sudan where some individual wild ass survived until recently, the animals have apparently totally disappeared.

The family occupies an isolated position within the order and is sharply differentiated from both the family Tapiridae (tapir) and family Rhinocerotidae (rhinoceros). The two latter families, though sharply distinguished from each other, are nonetheless closer than either family to Equidae.

The above phenomenon is largely explained by the separate existence over a long period and the independent evolution of horses, which originated either simultaneously, or almost so, with ancestors of early tapir and rhinoceros. Equidae have been found from the Lower Eocene of Europe and North America and the Miocene of Asia. The earliest forms belong to extinct subfamilies but present-day members (Equinae) have been found even in the Lower Miocene of North America. It is interesting to note that a significant part of their evolution occurred in the Americas, which could be considered the center of evolution of horses throughout the Tertiary period. Individual species and groups migrated from that continent to the Old World. However, for some inexplicable reason the group became totally extinct in the Pleistocene in both North and South America.

The composition of the family is simple. Three subfamilies are recognized: extinct Hyracotheriinae and Anchitheriinae and present-day Equinae. The family consists of 19 genera, of which only the genus *Equus* has survived. Six modern species are recognized (see characteristics of the genus), constituting 40% of the species of the order and about 0.2% of all mammalian species. Of these six species, four are African and two Asian.

The economic importance of various species of this family is presently negligible. Only some African species serve as objects of hunting. Some have become extinct (see characteristics of the order). Several species are totally or partly protected since their population is very small and still declining. Two species, horse (*"Equus caballus"*) and ass (*"Equus asinus"*), live in domestic and wild states.
696 Tarpan, widely understood as *E. przewalskii,* served as parent stock for the horse, and African wild ass (*E. africanus*) as parent stock for the ass; the latter is almost extinct today and apparently no longer found in a wild state.

The fauna of the Soviet Union include two species or 33% of the species of family Equidae, representing 0.6% of species of the Soviet fauna.

For the distribution of Equidae in the Soviet Union, see description of the order and genus *Equus.*

One of the two species is now extinct in the Soviet Union, while the other has survived in very small numbers and is totally protected. (V.H.)

Subfamily EQUINAE Steinmann and Döderlein, 1890

Genus of Horses

Genus *Equus* Linnaeus, 1758

1758. *Equus*. Linnaeus. *Syst. Naturae,* 10th ed., vol. 1, p. 73. *Equus caballus* Linnaeus (domestic horse).
1762. *Asinus*. Brisson. *Regn. Anim.,* p. 70. *Equus asinus* Linn. (domestic ass).
1762. *Onager*. Brisson. *Regn. Anim.,* p. 72. *Equus asinus* Linn. (domestic ass).
1924. *Microhippus*. Matschie. *Sitzungsber d. Ges. naturf. Freunde zu Berlin,* 1922, p. 68. *Microhippus tafeli* Matschie = *Equus hemionus kiang* Moorcr.[6]

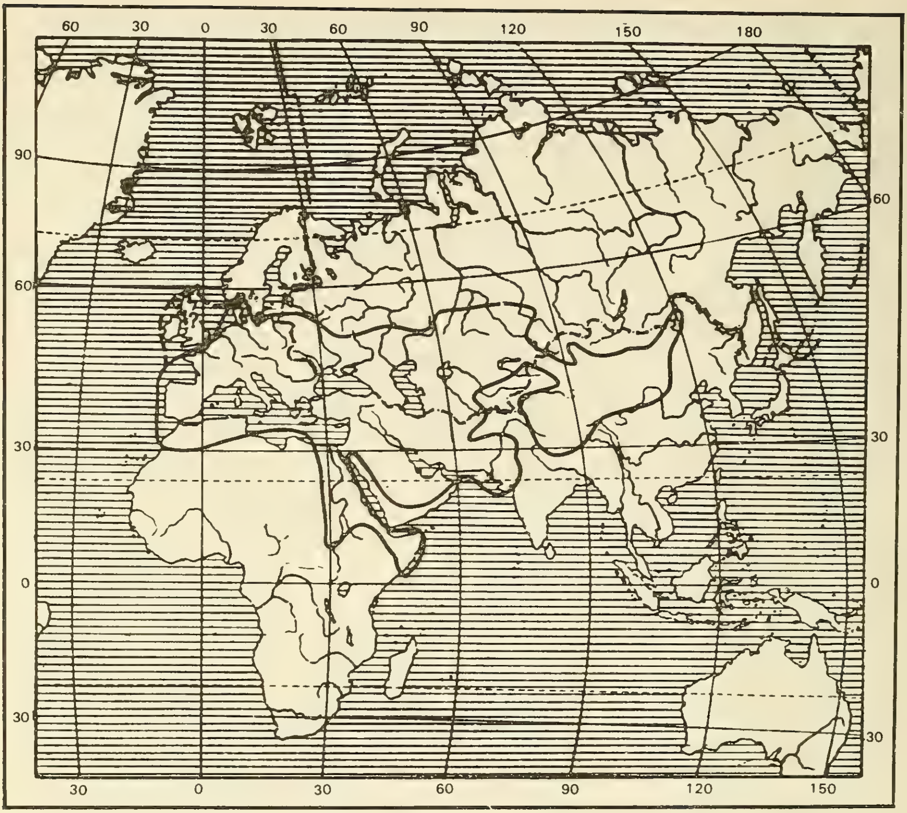
The morphological and geographic characteristics of the genus and family are identical.

Members of the genus are known from the Upper Pliocene when they were distributed in Eurasia, Africa, and North America. In North America horse disappeared in the Pleistocene. In South America they existed only in the Pleistocene (members of other genera lived there in the Pliocene). The lineage of the genus runs from *Merychippus* (Miocene of North America) through *Pliohippus* (Lower and Middle Pliocene of North America) and *Plesippus* (Upper Pliocene of North America). The latter group is so very close to *Equus* (particularly to *E. stenonis*; Gromova, 1949) that some regard it as directly transitional to *Equus,* while others even include it in this genus as a subgenus. Thus the genus *Equus* abandon the New World, and established itself in the Old World as a relatively recent immigrant. In the Old World horse evolved to a relatively small extent and formed a few branches exhibiting relatively weak divergence.

Attempts to split the genus into several genera have been made time and again but cannot really be justified. All the species form a fairly homogeneous unit in which some ill-defined groups can be segregated. At most, these could be considered subgenera, namely

---

[6] Several other generic (subgeneric) names are recognized but they pertain to species not represented in the Soviet fauna. *Asinus* pertains to African species but has been applied time and again to the Asian form (kulan) in English literature. The term *Hemionus* Cuvier, 1823 (or 1821), in relation to the kulan, is of no nomenclatural value since it has been used loosely ("hemione," Ellerman and Morrison-Scott, 1951).



697 Fig. 235. Reconstructed range of subgenus *Equus* L. s. str. (horse). V.G. Heptner.

the quagga group consisting of two species (steppe zebra or quagga, *E. quagga* Gm., 1788 and mountain zebra, *E. zebra* Linn., 1758—*Hippotigris*), Grevy's zebra group consisting of a lone species (*E. grevyi* Oust., 1882—*Dolichohippus*), true ass consisting of one species (*E. africanus* Fitz., 1857[7]—*Asinus*), and true horse consisting of two species (tarpan, *E. przewalskii* Pol., 1881 and kulan, *E. hemionus* Pall., 1775—*Equus* s. str.). The placement of the kulan with the ass (*Asinus*) or isolating it as a special subgenus cannot be condoned as either necessary or natural.

The genus consists of six species, listed above. Other systems of grouping horse into species have also been suggested but these do not differ much from that adopted here. Quite recently the Tibetan 697 kiang and Arabian kulan have been separated from the Russian kulan as a distinct species. However, this separation has now been discarded.

---

[7] The Linnaean name "*E. asinus* (1758)" pertains to domestic ass and hence has not been used here (see footnote no. 17 on pp. 539–40).

Two species occur in the Soviet Union—tarpan or wild horse, *Equus przewalskii* Poljakov, 1881 and kulan, *Equus hemionus* Pallas, 1775.

The range in the Soviet Union (reconstructed) covers the steppes of eastern Trans-Baikaliya, southern part of western Siberia and Kazakhstan, plains of Middle Asia, steppes and partly forest-steppes of the European part of the USSR in the north, at least to Voronezh, steppes of the Crimea and Cis-Caucasus, Belorussia, Lithuania, and plains of eastern Trans-Caucasus.

Tarpan are extinct within the Soviet Union and kulan totally protected.[8] (V.H.)

Key to Species of Genus Equus[9]

1 (4). Mane short and erect, forelock absent, much of tail base covered with short hair, with tuft of long hair at the end. In the skull auditory meatus elongated (its length more than width of third upper incisor), and clearly visible when skull examined from dorsal side.

698 2 (3). Color light yellow; white and dark transverse bands absent on shoulders. Size large (height at withers not less than 110 cm, body length from nose to tail base about 200 cm, and maximum skull length not less than 47 cm) . . . . kulan, **Equus hemionus.**

3 (2). Color gray, with a dark transverse field on shoulders. Size small . . . . domestic ass, **Equus asinus.**

4 (1). Mane long, falling onto neck; forelock present; tail with long hair from base. Auditory meatus in skull short and not visible when skull examined from dorsal side . . . . domestic horse, **Equus caballus.**

1. KULAN[10]

Equus (Equus) hemionus **Pallas, 1775**

1775. *Equus hemionus*. Pallas. *Novi Comment. Acad. Scient.*

---

[8] Additional information on the genus is given under the characteristics of the family.

[9] In the USSR only one species (kulan) is found in a wild state and is so well known that there is no need to define it. Sometimes, however, it becomes necessary to distinguish its skull, for which purpose the characteristics of domestic forms are given here.

[10] Kulan is a Turkmenian and Kazakh name. It is rarely used, mainly in old literature. The Mongolian name is "dzhigetai". The name "onager" is a wholly

Petropolitanae, vol. 19, p. 394, tab. 7. Lake Tarei-Nur, eastern Trans-Baikaliya.

1785. *Equus onager.* Boddaert. *Elenchus Animal,* p. 160. Kazvin [Gazvin], northwest of Teheran, northern Iran.

1904. *Equus onager castaneus.* Lydekker. *Novit. Zoolog.,* vol. 11, p. 590, plate XVIII. Khirgis-Nur, northwest Mongolia.

1911. *Equus (Asinus) hemionus finschii.* Matschie. "Zoologie (Nachtrag)" in Futterer's *Durch Asien,* vol. 3, pt. 5, p. 24. Site northeast of Lake Zaisan. (V.H.)

Diagnosis

Large-sized species with much of tail covered with short hair and long hair occurring in form of a tuft only at the end. Color yellowish, merging at places into white, with a sharp dark-colored stripe on the back; transverse dark field on shoulder blades absent. Ears moderate in length. Auditory meatus elongated and distinctly visible when skull examined from dorsal side. (V.H.)

Description

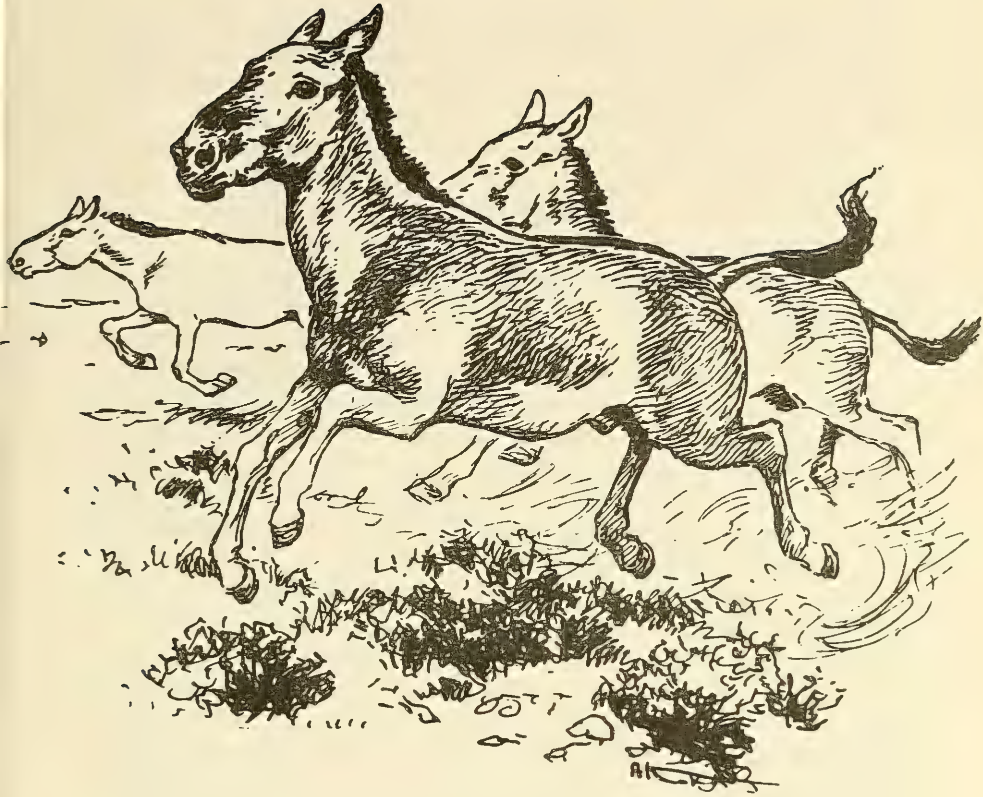
In general, build of kulan that of a typical horse—light, slender, and standing on fairly long legs. Head, however, relatively large and heavy, ears compared with those of horse somewhat elongated but much shorter than those of ass, and tail short with a tuft (as in zebra and ass). Anterior part of body relatively weak.

Summer coat very light-colored[11] and over most of the body light sandy-yellow. This very beautiful color in the fresh summer coat has tinges of apricot or orange shades; some individual body parts are white or creamy. Outer surface of thighs, sides of trunk, and much of neck and head vivid yellow. Stripe on thighs very bright and lower portion of yellow stripe on flanks lightens toward the back. Forehead more vivid in color. Abdomen and under surface of trunk, inner portions of legs, and rear and upper surfaces of thighs white. Outer surface of legs toward the top (region of crus and shoulders) yellowish, becoming white downward. White color on underside rises from groins in the form of a broad field between the yellow fields of thighs and flanks, dividing or almost dividing them and (to a somewhat lesser extent) runs upward along the shoulder blades. Narrow white

---

coined bookish name which should be discarded. Sometimes "kulan-onager" is used, which is totally unfounded and only pollutes the language.

[11] Description of south Turkmenian onager (*E. h. onager*).



699 Fig. 236. Onagers, *Equus (Equus) hemionus onager* Bodd. Sketch by A.N. Komarov.

699 field extends from large white speculum on rear of thighs along spine up to dark stripe. Lower surface of neck, head, and tip of muzzle white: dark lustrous skin visible between nostrils and on upper and lower lips. Ears white inside and light yellow outside. From the withers to the croup and farther along the back of the tail stump a narrow, but distinct blackish-brown stripe occurs, which somewhat, widens on the sacrum. Hair on this stripe slightly elongated.

From the region between the ears to the withers, a rather small, straight, dark-colored (black or blackish-brown) mane occurs. Forelock absent. Much of basal portion of tail covered with short light yellow hair and a large tuft of black hair present at end of tail. Tail short, not reaching hock or only just reaching it. Hooves dark-colored, small, narrow, hard, and straight set. Chestnuts present only on front legs. Eyes dark hazel. Wool short (about 1.0 cm), close-fitting, and glossy.

Coloration same in winter coat but duller and general shade darker and dirtyish. Hair long (about 2.5 cm), dense, and slightly wavy. Hair of stripe on back elongated and forms a small but prominent crest.

Skull of horse type. Auditory capsules with long meatus, length of which (from base to outer chamber) roughly 1.5 times greater than width of third upper incisor. When skull viewed from dorsal side, ends of meatus visible.[12] Their openings are fairly broad.

700 Body length of adult animals from tip of nose to base of tail 200 to 220 cm, tail length without terminal hair 43 to 49 cm and with terminal hair 60 to 99 cm, ear length 17 to 20 cm, and height at withers 110 to 137 cm. The young, up to the age of 1.5 months, have a body length of 110 to 120 cm, tail length 19 to 25 cm, ear length 17 to 20 cm, and height at withers 88 to 90 cm. Body length of animals aged 7 to 9 months 139 to 158 cm and height at withers 91 to 111 cm.[13]

Maximum skull length of adult animals 474 to 550 mm, condylobasal length of skull 445 to 488 mm, width of zygoma 182 to 209 mm, and length of upper tooth row 156 to 175 mm.

There are no sharp sex-related differences in measurements, but females are apparently somewhat smaller than males.

There are no significant age-related differences either, but juveniles in the first few months of life are relatively long-legged and long-eared and covered with a relatively long, soft, and slightly shaggy wool of a dull color. The relative length of limbs is particularly striking. Height at withers constitutes 75 to 80% of body length in the young versus 60 to 65% in adults. When compared to the length of the trunk, this disproportion is even sharper (Figs. 239 and 245).

Individual variability is very insignificant and involves some differences in size, general color intensity, and relative sizes of white and yellow bands. In over 50% of these animals P^1 ("wolf tooth") is absent and in the remainder highly variable in size. Sometimes it occurs on only one side. (V.H.)

Taxonomy

E. hemionus is a well and sharply characterized species occupying a fairly isolated position in the genus. Time and again attempts have been made to bring it close to *E. africanus* (ass) and include it in the same genus (subgenus) and species. There is no sufficient justification for doing this; it would be more correct to bring kulan closer to the true horse, *E. przewalskii,* in spite of some features of zebra and ass in kulan (also see section on tarpan). (V.H.)

---

[12] This is also the case in the domestic ass. In the domestic horse the auditory meatus is short and not visible from the top. Its orifice is narrow. Paired tubercles on top of symphysis of premaxillae, regarded as a characteristic feature of kulan (Bobrinskii, 1944), are often found in the horse also.

[13] Measurements from information available in literature, material of V.G. Heptner, and material from Badkhiz preserve (E.E. Shcherbina).

Geographic Distribution

Found in the steppe zone of the European part of the USSR, western Siberia, Kazakhstan, semideserts and deserts of Middle and Central Asia, Tibet, and steppes and desert regions of the Near East, including the Arabian Peninsula, Asia Minor, and northwest India.

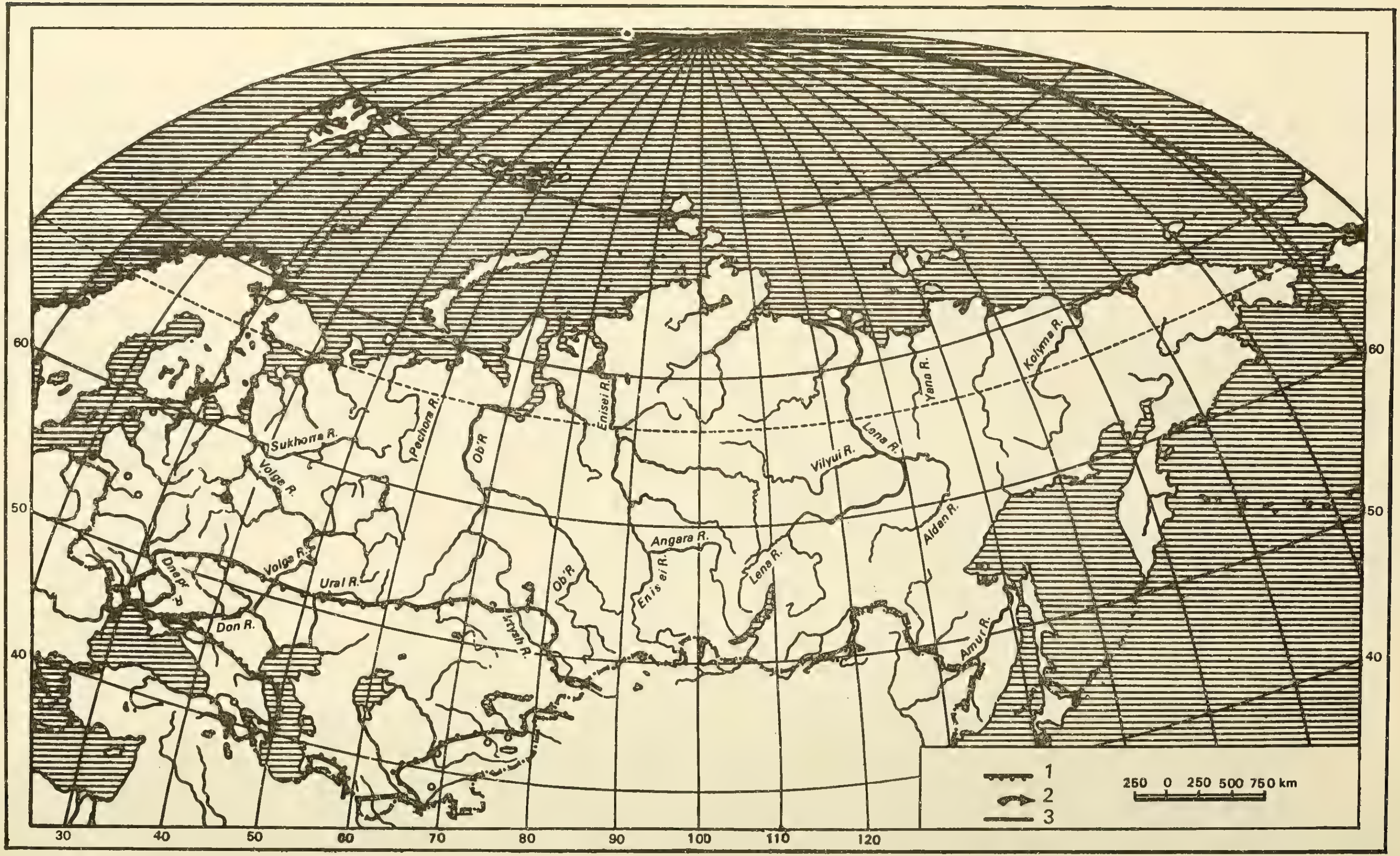
Over the historic period the range of the kulan has undergone great changes, toward reduction. These changes commenced apparently at the threshold of the present era, at places even earlier, and were particularly sharp and rapid in the last century. They proceeded even more intensely in the last 60 to 80 years and the animal is now extinct over much of the region of its distribution. The range, extensive before, has not only shrunk to an insignificant area, but also split into isolated pockets. The population of the animal, once very high, is now small even in these pockets.

The main reason for the reduction in the geographic distribution of kulan is extermination and squeezing out brought about by steadily increasing human colonization of steppes and semideserts, and recently even of deserts formerly uninhabited or only slightly inhabited. The extensive use of long-range firearms, and primarily the nonavailability of water holes for these animals due to the development of animal husbandry, as well as inadequate protection, or the absence of any protection at all, have played a decisive role in the reduction of the range. The recent introduction of automobiles into the desert and their use in hunting has also contributed to this reduction. The kulan is one species whose range has shrunk dramatically.

Geographic Range in the Soviet Union

702 The range in the Soviet Union (reconstructed) covers desert, semidesert, and steppe zones, and part of the forest-steppe. Much of the northern and northwestern parts of the range of the species, roughly one-third or more, fall within the USSR. The range consists of three sections isolated from each other within the Soviet Union: Trans-Baikaliya, Middle Asiatic, and Trans-Caucasian.

In Trans-Baikaliya the range covers only a small section at Lake Tarei-Nur (Zun-Tarei), north of Solovev, and the steppes along the



Sukhona R.
Pechora R.
Ob'R
Enisei R.
Yana R.
Kolyma R.
Lena R.
Vilyui R.
Volga R.
Volga R.
Dnepr R.
Ural R.
Don R.
Irtysh R.
Ob'R.
Enisei R.
Angara R.
Lena R.
Aldan R.
Amur R.
60
50
40
60
50
40
30
40
50
60
70
80
90
100
110
120
1
2
3
250 0 250 500 750 km

Argun to the north of Lake Dalai-Nur in Manchuria. This projection of the Mongolian-Manchurian zone represents the northernmost extremity of the range of the species.

Even in the latter half of the eighteenth century these animals did not settle in Trans-Baikaliya but only visited it. Visitations occurred in summer, especially with a scarcity of food in the south (Pallas, 1774 and 1811). Yet even in the middle of the nineteenth century these animals were very common within the Soviet Union (Radde, 1862; Cherkasov, 1867; V. Skalon, 1949). They disappeared in the latter half of the century. This is associated with a significant withdrawal of the northern boundary of distribution into Mongolia and Manchuria. From the end of the nineteenth century to the early twentieth century only one chance intrusion of a kulan within the territory of the Soviet Union occurred; this was in 1926 (V. Skalon, 1949).

Kulan evidently existed even in western Trans-Baikaliya but in the far remote past; their remains have been found in burial mounds from the third century B.C. (V. Skalon, 1949).

The Trans-Caucasian section of the range of kulan is also very small but somewhat larger than the Trans-Baikal one. It covered the northern rim of the Iranian-Asia Minor part of the range. This section in turn was apparently divided into two parts. One, the smaller, covered a small expanse in the Araks steppe of Armenia, i.e., the region lying north of Ararat (Sarkisov, 1946). The other part occupied the steppes of the eastern Trans-Caucasus. Details of the distribution of kulan there are not available but there is no doubt that it covered all of the plains of the country and extended in the north to the Apsheron Peninsula (Vereshchagin, 1947). In Armenia kulan survived at least to the eleventh century and in the eastern Trans-Caucasus to the twelfth (Baku; Vereshchagin, 1947).

The main habitat of kulan in the Soviet Union, the Middle Asiatic region, covered the desert and semidesert plains of Middle Asia and Kazakhstan and partly the steppes of Kazakhstan, western Siberia, and the European part of the USSR. In the south the range extended to the Kopet-Dag and the foothills of the Pamir-Alai and Tien Shan systems, and in southern Turkmeniya between the Amu Darya and Tedzhen and also extended from the USSR into Afghanistan and Iran

---

701 Fig. 237. Distribution of kulan, *Equus (Equus) hemionus* Pall., in the Soviet Union.

1—reconstructed boundary in historic period, including also region of fairly regular dispersal in the north and west; 2—dispersal of kulan in the eighteenth century in Barabin steppe; 3—approximate northern boundary of contemporary habitat including permanent transgressions. V.G. Heptner.

along the lower reaches of the Artek. In the east, in Dzhungaria and the Lake Zaisan regions, the range passed in the form of a narrow strip through Dzhungaria to join the Central Asiatic habitat.

The northern boundary of distribution of kulan in Kazakhstan and western Siberia cannot be established with certainty, primarily because of inadequate information relating to the remote past. Moreover, in the northern part of the region of distribution kulan underwent regular seasonal migrations in the summer northward and in winter far southward. The amplitude of these migrations reached 500 to 600 km or more. In some years, or over a series of years, kulan migrated far north beyond the limits of its normal summer residence. There are also records of finds of single animals or troops at far-away places.

As a typical desert and semidesert animal kulan normally did not reach the northern extremity of the steppes and did not survive in the region of forest-steppes. During summer they apparently dispersed only up to the northern extremity of the semidesert, i.e., roughly up to 50° N lat. At the same time they penetrated quite often into the steppe zone, primarily into the region of turf-grass steppe. It may be assumed that between the Irtysh and Ural, the northern boundary of distribution of kulan, including their more or less frequent transgressions in the historic period, reached to slightly south of 52° N lat. or along this parallel. At some places kulan, however, penetrated even farther, for example, to the Kokchetav ("Kukchinsk"; Rychkov, 1762) hills (about 54° N lat.). In the west they occurred on the steppes in the eastern foothills of the southern extremity of the Urals. The animals evidently did not cross to the north of the longitudinal course of Ural River.

703 In the east, beyond the Irtysh, kulan were present north and northeast of Zaisan, at Semipalatinsk, in the Cis-Altai steppes, and in the Kulunda steppe. In the latter two regions the animals occurred apparently more as transients. Transgressions are known even in the Barabin steppe, i.e., significantly to the north of 52° N lat., probably to 54° N lat. In winter in the expanse between the Ural River and the Altai kulan reached south beyond 48° N lat. where the snow cover is discontinuous.

In the west kulan colonized not only the steppes, but probably also the southern fringe of the forest-steppes in the European part of the USSR. The northern limit of the range there ran probably initially at the same level as in western Kazakhstan, i.e., at the level of the longitudinal course of the Ural (about 51 to 52° N lat.). At this latitude they probably reached even the Voronezh region but farther west descended to the latitude of Kiev, more to the south. From there they moved south along the boundary of the densely forest-covered regions of the western Ukraine. In the southwest kulan reached the lower reaches of Bug and probably the Prut. In the south the range extended to the Azov and Black Seas and covered the Cis-Caucasian steppes.

No details whatsoever are available about the distribution and nature of the residence of kulan in the European part of the USSR and factual data, in general, are scanty. Data are available about the occurrence of "onager" at the turn of this era only for Skifia, i.e., in the Black Sea steppes (Strabo), and remains of kulan are known from Ol'via (Bug estuary, start of this era; Pidoplichko, 1951). Later remains of kulan pertaining to the twelfth century have been found in Vyshgorod at Kiev (Zubareva, 1940); it has been suggested that some frescoes in the Sofian cathedral are of kulan (early twelfth century; Charlemagne, 1949).[14]

The distribution outlined above is essentially tentative. In the European part of the USSR, west of the Volga, kulan were probably few in number everywhere and only visited some parts of the region, primarily the northern and westernmost sections. The European part of the USSR is less favorable for kulan because of the fewer possibilities for winter migrations southward there (sea) than in Kazakhstan. The winter climate is also quite severe. Kulan were evidently more common in the easternmost parts of the country, in the region between the Ural and Volga, and in Cis-Caucasus and Kalmyk steppes, which corresponded for the animal to desert and semidesert conditions.

Some zoologists state that kulan occurred in the western parts of the Ukraine, Belorussia, and Lithuania even in the sixteenth, seventeenth, and eighteenth centuries (Charlemagne, 1949; Pidoplichko, 1951). This is incorrect and based on a misunderstanding of reports of older writers. "The assumption that the references of M. Litvin, Mekhovskii, and Gerbershtein should be construed as pertaining to wild

[14] Finds of kulan remains around Kiev by Korneev (1953) have not been accurately dated and pertain evidently to the prehistoric period. Kulan remains of the Tripol' period are known from around Odessa and the Bronze Age from the Don River (Pidoplichko, 1951).

Information about the occurrence in the Voronezh region of a second species of wild horse (apart from tarpan) given by S.G. Gmelin (1771) is extremely confused and should not be regarded as positively referring to kulan as is sometimes done (Charlemagne, 1949). Gmelin himself saw in Voronezh province only tarpan; he was only told that horses with very long and downcast ears like those of ass had been sighted there. It should be pointed out that the kulan is not such a long-eared animal as sometimes thought and in any case is not like the ass. Its head is far more similar to that of a horse. Kulan usually hold their ears like a horse and do not droop them. The most striking visual difference between kulan and tarpan is the coat and not the ears. Tarpan sport a uniformly dark gray color. Gmelin says nothing about the animal's coat.

ass is erroneous. These references indubitably refer to horse. Gershtein himself in listing animals present at that time in Lithuanian forests placed among them 'horses, also sometimes called onager' ". Kromer in his *Polonia,* written in 1578, points out that the horse was sometimes incorrectly labeled onager (onager, vel los apellatur; alcem hanc esse volunt). Rzhonchinskii also points out that "because of its similarity to mule, some called the moose an onager (et quia est similis mulo placuit quibusdam ut onagrus diceretur)" (S.V. Kirikov). In the contemporary context this strange habit of giving an ordinary animal an alien name can be explained by a desire to fit available information under that of older authors, a tendency arising in the Middle Ages which continued sometimes through the sixteenth to the eighteenth centuries. The occurrence of kulan in
704 Lithuania and Belorussia, at that time considered countries covered by extensive forests, is improbable even from a purely zoological point of view.

In the Ukraine kulan disappeared probably soon after the above dates; there is no recorded proof of their survival in subsequent centuries. If not simultaneously, still quite long ago, these animals disappeared even from the Don basin; information about their occurrence in the Voronezh region in the eighteenth century, as already mentioned, is unreliable. Exceptionally, in the eighteenth century, kulan may have been sighted in these places as very rare intruders. Kulan were preserved longest, i.e., even in the eighteenth century, in deserts between the Volga and Ural (Pallas, 1786). There they possibly survived up to the nineteenth century.

In Kazakhstan population reduction and range shrinkage southward were observed long ago. Furthermore, in the eighteenth century kulan had a far more continuous distribution, covering much of Kazakhstan and the Middle Asian plains in the south up to the state boundary, mountain systems in the above areas, and cultivated lands in the extensive submontane oases (Tashkent, Bukhara, and others). They were distributed even farther northward and found, for example, around Semipalatinsk and along the Irtysh to 52° N lat. In Kazakhstan in the mid-1700's kulan were abundant around the Sarysu River; "I met with them at that time also along the Emba River and in Eremei and Kukchin mountains"[15] (P. Rychkov, 1762). In the 1860's it was reported (Zavalishin, 1867; Krasovskii, 1868) that kulan were no longer seen in the northern extremity of Kazakhstan. The extreme northern limit of their range in the 1870's through the 1890's was represented by the spurs of the Mugodzhar and Ulutau, the Kulan-Utmes River, and the tributaries of the Terisakkan River

---

[15] Kokchetav and Ermentau mountains (V.H.).

(Slovtsov, 1897; Stepnyak, 1896). The Ural River at Reduts outpost was the western limit of occurrence at the end of the 1860's (Karelin, 1875). But close to this river "kulan were occasionally seen while herds usually grazed beyond 100 versts of the river (N.A. Severtsov, 1861)" (S.V. Kirikov).

By the early twentieth century over much of Kazakhstan the kulan had already completely disappeared and survived only in the extreme eastern part, i.e., in the Bet-Pak-Dala, northern and southern Pri-Balkhash, Dzhungarian Gate, and Zaisan depression. At places, e.g., Bet-Pak-Dala (von Hern, 1891), the animals were even quite numerous.

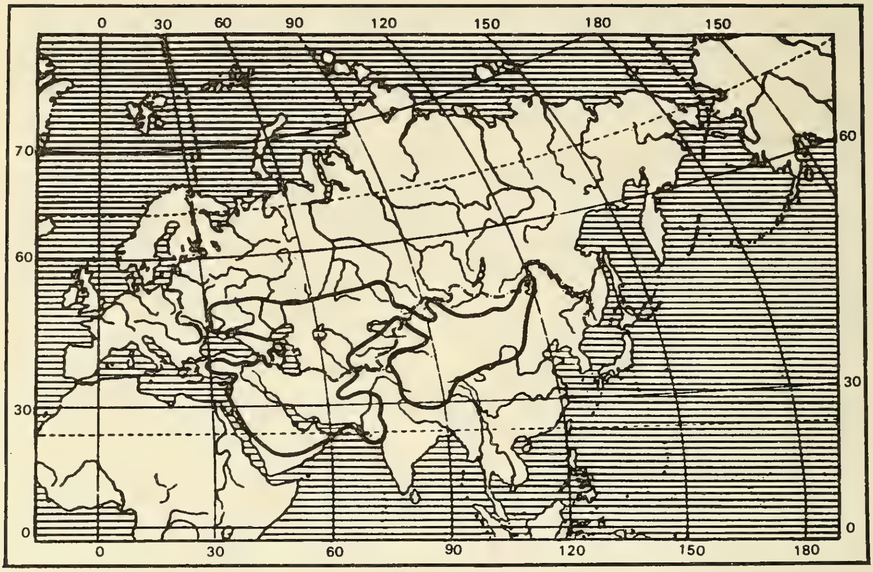
By that time kulan still survived in the west along the eastern bank of the Caspian Sea from Mangyshlak to Atrek and lived throughout the plain adjoining Kopet-Dag on the north and in the expanse of southern Turkmenia between the Tedzhen and Murgab, and the Murgab and Amu Darya. Details about their existence in this area are few indeed. Probably they were encountered in the Ustyurt but did not survive deep inside the sandy deserts. Kulan were no longer sighted in the Kyzylkum at this time. Hence by the early 1900's the Middle Asiatic and European ranges had not only decreased sharply in size, but the formerly continuous range had split into two isolated sections—Pri-Balkhash and Turkmenia.

The Pri-Balkhash section of the range continued to shrink rapidly and the population of kulan declined. The animals had disappeared almost everywhere even in the 1920's and only a small number were reported in southern Pri-Balkhash in the 1930's. By the end of that decade they had disappeared even there. During the 1930's and later stray intrusions were reported from Dzhungaria into the eastern extremity of Balkhash, along the Ili, and into the spurs of the Dzhungar Alatau (E. Strautman, 1953).

In the Turkmenian section the range withdrew eastward from the sea coast. Even in the 1910's the animals were sighted throughout the Kopet-Dag plains. By the 1920's sightings were already rare and occurred only in the eastern part (east of Ashkhabad). During the 1930's the animals disappeared even there and survived from then onward only in Badkhiz, i.e., the region between the Tedzhen and Murgab south of the Serakhs-Sary-Yaza line (Badkhiz preserve and adjoining sites). There is no precise information about the
705 occurrence of kulan east of Murgab but it is possible that some still survive south of the line Sary-Yaza-Kerki on the Amu Darya. Animals straying from Dzhungaria into Pri-Balkhash are not ruled out.[16]

---

[16] The distribution in Middle Asia, unless otherwise stated, is based on material collected and data compiled by V.G. Heptner.



705 Fig. 238. Reconstructed range of kulan, *Equus (Equus) Hemionus* Pall. Schematic. Much of boundary tentative. V.G. Heptner.

In the Paleolithic period kulan were encountered on the Yenisey (Afontova mountain; 200 km above Krasnoyarsk), the Altai, and in Trans-Baikaliya (V.L. Gromova, 1948). These areas fall outside the present reconstructed range of kulan within the Soviet Union.

Geographic Range outside the Soviet Union

Outside the Soviet Union kulan are found in the western edge of northeastern China, the Mongolian Republic except the northern montane regions (Khentei and Khangai), Inner Mongolia, Dzhungaria, Kashgar, Tibet, northern Nepal, Ladakh, Sind and Cutch in northeastern India, Baluchistan, Afghanistan except montane regions, Iran, Asia Minor, Iraq, Syrian region of the United Arab Republic, and the Arabian Peninsula.

Today the range is considerably smaller: kulan are totally extinct in Asia Minor and over much of the Arabian Peninsula, extinct or almost so in the Syrian region of the United Arab Republic, extinct in Mesopotamia, highly reduced in Iran, and extinct or almost so in India and Baluchistan. Kulan have disappeared from northeast China and their range has withdrawn significantly southward into the Mongolian Republic. Their range in Inner Mongolia, Kashgar, and Tibet is still shrinking. Unless protective measures are implemented soon the species is threatened with rapid extinction. (V.H.)

Geographic Variation

Only a cursory study of the intraspecific variability of kulan has been done to date. This is primarily due to the scanty material of this species available in collections. Moreover, because of total extinction, the species is generally absent over large expanses. Hence it is no longer possible to judge the characteristics of the animals which inhabited those areas.

A large number of names (about 20) have been given to the species, some simply popular synonyms. Only a few are of consequence. Until the last decade usually two or three species of kulan were recognized (*E. kiang, E. hemionus,* and *E. onager*; Lydekker, 706 1916; sometimes the form *hemippus* was also isolated as a separate species). Nowadays the species is generally interpreted in the manner accepted here.

The total number of races is usually considered six (Lydekker, 1916; Harper, 1945) or five (Haltenorth and Trenze, 1956). Features distinguishing the different forms are, however, apparently far less significant than generally thought and it is highly possible that the number of true subspecies is less. Within the species three groups are undisputedly distinct: relatively large and dark-colored Tibetan kiang (*kiang*), very diminutive and extremely light-colored kulan of the Arabian Peninsula (*hemippus*), and kulan of the Middle East and Central Asia, Mongolia, and Kashgar (groups *hemionus* and *onager*)—together constituting a group somewhat intermediate between the first two in body size and color. The placement of some forms in the third group, which usually comprises four subspecies, is debatable, especially since various taxonomists interpret them differently.

Within the USSR three forms of kulan may be recognized tentatively.

1. Mongolian kulan, *E. h. hemionus* Pallas, 1775.

Size large. Body length from nose to base of tail up to 220 cm, tail length without terminal hair 43 to 49 cm and with it 92 to 99 cm, and height at withers about 127 to 137 cm; maximum skull length 466 to 550 cm, condylobasal length 448 to 488 mm, width of zygoma 182 to 209 mm, and length of upper row of molariform teeth 160 to 175 mm (Allen, 1940; material from central Mongolia).

Color relatively dark. White fields on groins and in scapular region weakly expressed. Yellow field on thighs extensive and merges into single field with that on flanks. Light-colored sections often not white but creamy. White field along stripe on back absent, poorly defined, or visible only in posterior third of animal's body.

This form (now absent) was formerly found in Trans-Baikaliya. Outside the USSR it is still found in Mongolia and other parts of the species range—Central Asia, except Tibet, and probably Dzhungaria. It is possible that the range extends even farther westward (see below).

2. Kazakhstan kulan, *E. h. finschii* Matschie, 1911 (the name *castaneus* has also been used for this form). Fairly large and relatively dark-colored form, apparently only slightly lighter in color than the preceding one. Sizewise the two forms are comparable.

Steppes of Kazakhstan and western Siberia but at present not in the USSR. Outside the Soviet Union it may survive in Dzhungaria.

The independent status of this form in relation to the preceding one has not yet been established and appears dubious. It is highly possible that the Mongolian form (nominal form) inhabited the steppes of Kazakhstan and western Siberia. It is possible that it also penetrated the European part of the USSR, although the possibility is not excluded, that the true form lived here. Because information on the second form in the museums of Kazakhstan is negligible, and its disappearance from the European part of the range, this question cannot be resolved. The affinities of the forms *finschii* and *onager* are also not clearly understood (see below).

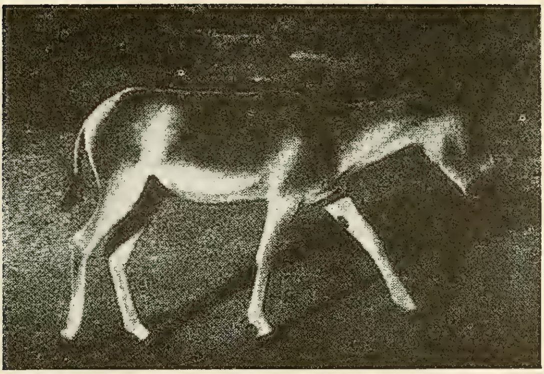
3. Turkmenian kulan, *E. h. onager* Boddaert, 1785.

Relatively small in size. Height at shoulders 110 to 120 cm. Maximum skull length 474 to 522 mm, condylobasal length 445 to 492 mm, width of zygoma 190 to 209 mm, and length of upper row of molariform teeth 152 to 174 mm (based on four adult animals from southern Turkmenia).

707 The color of this form is very light and the white fields highly developed (see above for description).

Found in Turkmenia and southern parts of Middle Asia, eastern Caucasus, and Armenia. At present found in the Soviet Union only in the extreme south of Turkmenia in the region adjoining Afghanistan, along the upper Tedzhen and Murgab. Outside the Soviet Union found in Afghanistan (at least the northern part of it) and over much of Iran (except the extreme southeast).

The taxonomic affinities of Turkmenian and Kazakhstan forms are poorly known since no accurate analysis of them has been made to date. The differences given above thus require confirmation. At least the kulan of extreme southern Middle Asia is likely to differ from that of Kazakhstan. How far north the form penetrated, where and how it came into contact with *finschii*, which form lived in the north on the eastern coasts of the Caspian Sea—these are questions for which no information is available and a resolution no longer possible.



706 Fig. 239. Turkmenian kulan, three-year-old stallion. Nursery of Badkhiz preserve (southern Turkmenia). May, 1948. Photograph by V.G. Heptner.

The following forms are usually shown in some parts of the range outside the Soviet Union. Kiang or Tibetan kulan, *E. h. kiang* Moorcr., 1841 (Ladakh, Nepal, Sikkim, and Tibet, to the Kukunor region); Indian kulan, *E. h. khur* Less., 1827 (northwest India, Cutch, possibly Baluchistan, and southeast Iran); Arabian or Syrian kulan, *E. h. hemippus* I. Geoffr., 1855 (Arabian and Syrian deserts) (apparently totally extinct now or only very few have survived); and Asia Minor kulan, *E. h. anatolica*[17] (Asia Minor) (extinct in the last century).

It is quite likely that the form *khur* should be merged with *onager*. The Asia Minor kulan probably belongs to the same type.

The geographic variability of kulan reflects Bergmann's, and in part Gloger's rules. (V.H.)

Biology

Population. At present (1940's and 1950's), kulan inhabit about 8,000 km^2 in the Badkhiz (interfluve region of upper Murgab and Tedzhen). During the summer–autumn period, from June through November, the number of kulan living in this region evidently does not exceed 600. According to calculations made at water holes in October, 1952, 158 animals inhabited an area of 7,000 km^2. In September, 1953, 96 animals were counted from an airplane over an area of 4,056 km^2. The mean density from these data yields one animal

---

[17] This form has only recently been suggested (Haltenorth and Trenze, 1956) and no formal description published as yet.

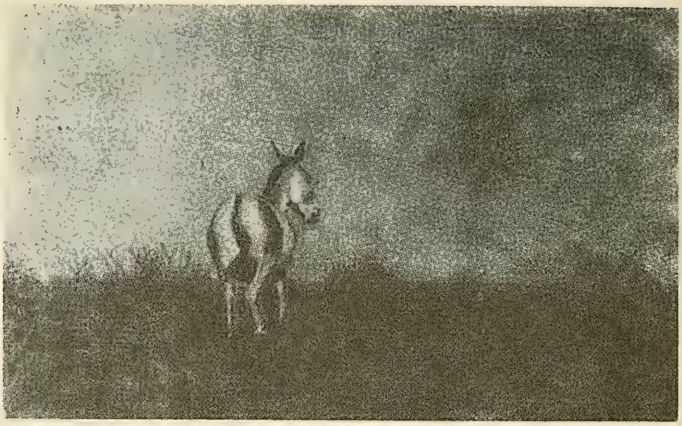


Fig. 240. Kulan in Badkhiz preserve. Photograph by A.O. Solomatin.

per 42 km^2 (Shcherbina, 1953). During the winter–spring period, when the animals no longer need water holes, their population in 708 the Badkhiz usually increases because of migrations of some individuals from Afghanistan. In the winter of 1956 in Badkhiz about 400 animals were counted (Kravchenko and Shcherbina, 1959); they numbered 600 in 1957 and 500 in 1958 (Solomatin, 1959).

In the past kulan were more numerous. Even at the beginning of this century herds of 100 or more animals were sighted in the Badkhiz (Gromov, 1937; Heptner, 1948). Congregations in the past of thousands of kulan at wintering sites in northern Kazakhstan have been indicated (Sludskii, 1953).

Habitat. Kulan inhabit the plains or hilly-ridged deserts and semideserts. In the Badkhiz they are confined to plains and gentle hill slopes to a height of 300 to 600 m above sea level. During snowstorms and duststorms they find refuge in narrow valley. They avoid loose and shifting sands, which are difficult to negotiate, and where food is scarce.

Kulan inhabit places with a very diverse plant canopy but prefer rich semidesert pastures such as grass-sagebrush and grass-saltwort. In Badkhiz the animal is confined to ephemeral sagebrush with an abundance of meadow grass, admixture of narrow-leaved sedges, semishrubs, ephemerals, and rare Umbelliferae, i.e., *Ferula.* From time to time it penetrates succulent saltwort associations in pistachio plantations in elevated sections of the Badkhiz. In Mongolia in summer it inhabits grass-onion semideserts and grass-saltwort and grass-saltwort-sagebrush-rubble deserts. In winter it occurs in shrubby deserts and feather grass forb steppes. The latter were

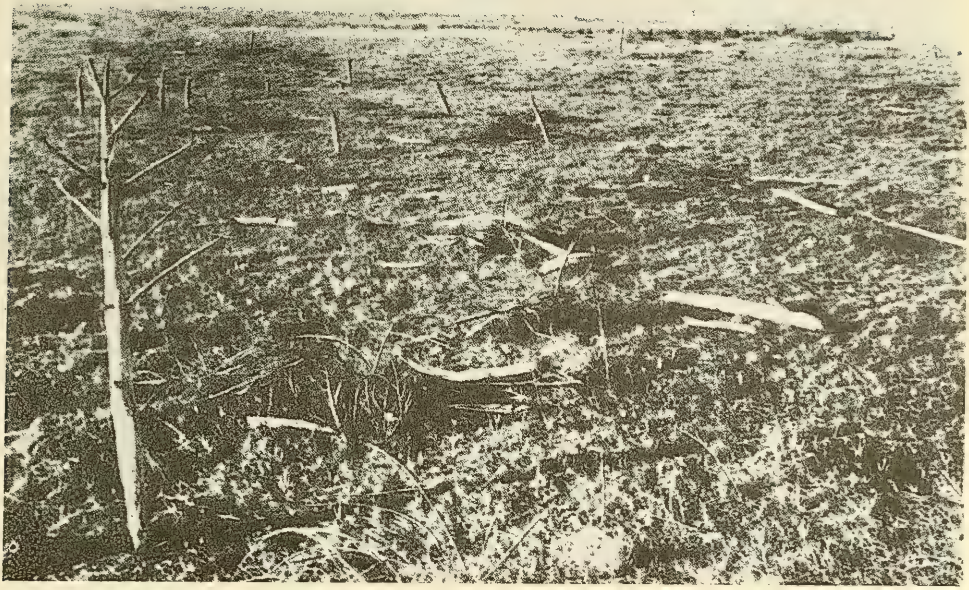


Fig. 241. Habitat of kulan in Badkhiz desert (southern Turkmenia). Stalks of year-old fennels (*Ferula badrakema*), mainly fallen ones, visible. June, 1948. Photograph by V.G. Heptner.

important in the past when the kulan population was high and the species more widely distributed in Kazakhstan (Slovtsov, 1897), Trans-Baikaliya (Radde, 1862), and Mongolia. At present this is reported only from China.

Food. The food of kulan has not been thoroughly studied. This species mainly feeds on herbaceous vegetation and avoids coarse browse foods. In summer the main diet consists of grasses such as meadow grass, sedge, ephemeral feather grass, onions, and forbs. In autumn sagebrush and succulent saltworts play the main role. In winter the importance of grasses increases again, and sagebrush, 709 forbs, and shrub saltworts constitute a high percentage of the food ration. In the Badkhiz the main food year-round is meadow grass and sedges (V.G. Heptner), while substitute foods comprise shrub saltworts, camel's needles, and the fruits of saxaul (Shcherbina, 1951). In all, 10 to 12 species of plants are known to be consumed by kulan. When the thickness of the snow cover exceeds 10 cm, access to food becomes difficult.

In Kazakhstan the favorite food plants were biyurgun *Anabasis salsa, Ceratocarpus arenarius, Atriplex cana,* and the treelike saltwort *Haloxylon arborescens* (Slovtsov, 1897). In Mongolia feather grass, onions, and *Anabasis brevifolia* constitute the most important summer foods, and semishrubs and shrubs play a lesser role. These include bean caper, ephedra, and shrub saltwort. In all, 12 to 15 plants are known to be consumed but do not constitute an exhaustive list by any stretch of the imagination (Bannikov, 1948).

For the greater part of the year water holes are essential for kulan. The animal is less dependent on them only in winter and spring when snow or puddles and green vegetation provide fairly abundant moisture. In the dry and particularly warm period of the year water holes are of utmost importance to kulan and determine their distribution within a territory, daily rhythm, and behavior (Bannikov, 1948; Heptner, 1948). When open water sources within 15 to 20 km in a region to which a herd is confined are available, the animals visit them daily, mostly in the evening or at sunset. Herds living some tens of kilometers away from water holes probably do without water for two or three days at a time, but water holes nonetheless represent an essential condition for existence. In deserts where there are no available sources, kulan are also absent in summer. It may be said that water holes are the major factor governing the present-day distribution and population number of the species in Turkmenia, Mongolia, and most other countries. Reduction of available sources accessible to the animals, as a result of human settlements together with livestock, have resulted in the displacement of kulan from most regions (Heptner, 1948; Bannikov, 1948). Kulan lap brackish-saline water which even camels and asses reject.

Home range. The size of the home range of the animals is not precisely known. Their study is complicated by changes in individual sections in different seasons, their herding pattern, seasonal migrations, population changes in different habitats brought about by the state of pasture, and the availability of water holes.

In summer kulan herds are confined within a radius of 10 to 15 km from a water source. Furthermore, at places where the animal is not disturbed and pastures are rich, they remain at one given place for many months. In winter, with an overall depletion of pasture but an abundance of water holes everywhere, the area of occupation of the animals increases at least by five- to sixfold. Quite often herds wander widely or such migrations of many herds may take the form of seasonal shifts (Bannikov, 1959).

Daily activity and behavior. Kulan graze throughout the day without a rest at midday, moving nonstop slowly over pastures. From time to time they flop down and squirm in dusty areas to free themselves of insects. They spend the night in beds located usually

among sparse and low bushes. They leave the beds at dawn and, if a water hole is close by, move toward it slowly. By the time the sun is up they have returned to the desert. Similarly in the evenings herds move lazily to water holes where they remain until sunset. Quite often they use the same pathways to reach water sources. In the event of danger the stallion first takes to a gallop, but if the herd is well spread soon returns and neighs a warning to females and young, or nudges them into flight with light bites and characteristic head movements. When a female is killed, the male leads the rest of the herd away to safety, then returns to the dead female and circles her for quite some time, neighing off and on. When a herd is chased, the animals attempt to cross the course of the rider or automobile, sometimes repeating this maneuver two or three times. Kulan can attain a
710 speed of 60 to 70 km an hour and run up to 10 km at this speed; they can run much longer distances at a speed of 40 to 50 km per hour (Bannikov, 1955). Galloping horses and relay chases, using the best of horses, did not prove successful in chasing a kulan throughout an entire day (Heptner, 1948). Kulan can easily negotiate a snow cover 20 to 25 cm thick (Polferov, 1896), but their movements are impeded by a depth of 30 to 35 cm.

The kulan is an extremely alert and cautious animal and approaching it in an open desert is impossible. Generally, though, the proximity of man and domestic cattle has no perceptible adverse influence if the animal is not pursued. Kulan sometimes graze close to herds of horses and flocks of sheep. At the same time, even when extremely thirsty, they will not go to water sources used by man and livestock.

During summer and early autumn kulan troops consist of a stallion, females, and juveniles of the first and second years. Some females with newborn foals separate from the troop during May through July. During rut solitary males are seen, mostly those which take part in reproduction for the first time. In autumn and winter troops merge into a herd, the size of which depends on the overall kulan population in a given region.

The average number of animals in summer troops, according to counts made in the Badkhiz in 1953, was 8.7 animals. Most often, troops of 10 to 20 animals or lone animals were encountered. The maximum size of a herd in the Badkhiz did not exceed 200 animals (Shcherbina, 1953). According to the data of Ishunin and Korovin (1945) and Heptner (1948) kulan troops in the Badkhiz consisted of 10 to 15 animals each; lone animals and groups of 3 or 4 were quite common. Herds of over 100 animals were seen only during late autumn migrations. In Kazakhstan (Nikol'skii, 1887; Slovtsov, 1897)

Fig. 242. Spring pasture in Badkhiz preserve. Photograph by A.O. Solomatin.

summer troops were roughly the same size as in the Badkhiz. In May and June, from time to time, females with young or males grazing separately have been observed. Von Hern (1905) mentions troops of up to 40 animals sighted in Bet-Pak-Dala. Autumn–winter congregations there numbered thousands of animals. In Mongolia the average number of animals in a summer troop was 11, but in good pastures in autumn these troops often joined together into herds of several hundred animals (Bannikov, 1948). Such herds, comprising hundreds of kulan, formed in Trans-Baikaliya in the eighteenth century (Pallas, 1771), but by the mid-1800's the number of animals in a troop rarely exceeded several dozen (Radde, 1862). Detailed information about the age and sex composition of troops is very scanty. Eight troops with a total population of 58 animals encountered in Mongolia in June–July showed the following average composition: number of animals per troop—8.0; adult males—1.0; adult females per male—3.8; and juveniles (one to two years old)—2.3.

711 *Seasonal migrations and transgressions.* Until recently in Badkhiz migrations of some animals from the northern (Soviet) Badkhiz into the southern (Afghan) Badkhiz and back were not uncommon. In summer kulan moved southward where large exposed water sources are accessible. These migrations southward depended on the summer disposition of sheep flocks around the water holes in the Soviet Badkhiz and varied significantly (Heptner, 1948; Shcherbina, 1951). In 1958, when most of the available water sources in the northern Badkhiz were occupied by sheep flocks, most kulan moved off into the Afghan Badkhiz (Solomatin, 1959). Migration commenced toward the end of June to early July, and reverse movement in November. A significant percentage of the Badkhiz population lead

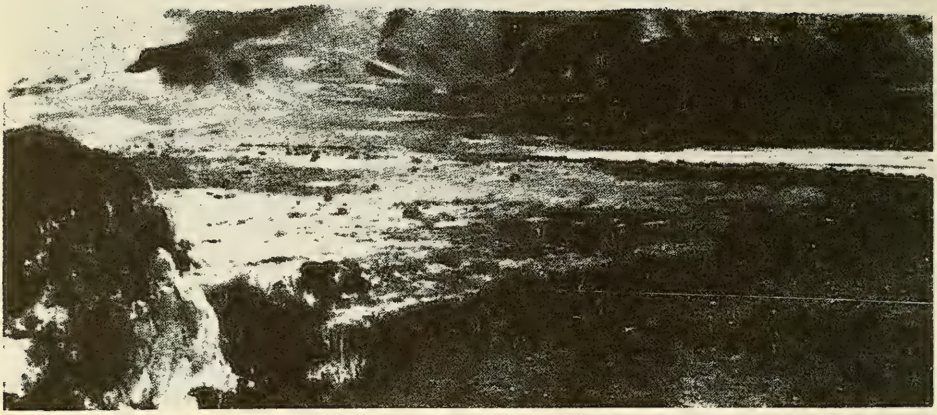
a settled life. Conditions for wintering of kulan in the Soviet Badkhiz are apparently better than in the Afghan Badkhiz. There, on the plateau of Lake Er-oilan-duz basin and Namaksaar, as also in the Duzen-Kyr and Elle-Bir hills, the majority of northern Badkhiz kulan and a significant number of southern Badkhiz kulan as well used to congregate. In some years, for example 1957, herds of up to 100 animals have arrived there from Afghanistan. These regions provide good pastures of sedges and grass (meadow grass); the rugged relief itself provides refuge from adverse weather conditions. Mass foaling occurs there in spring (Solomatin, 1959).

Congregations of kulan in regions where water holes are available in summer, and far wider migrations during the period when the animals have little need for water, are common everywhere. In the past, over much of Turkmenia and southern Kazakhstan, as also even now in the deserts of Mongolia and China, kulan undertook only such migrations and spent a fairly settled way of life. On the contrary, in northern Kazakhstan, northern Mongolia, and Trans-Baikaliya, seasonal movements were in the nature of regular migrations over long distances. Furthermore, the general direction of autumn migration, i.e., migration into the western (Kazakhstan) part of the range and into the eastern (Mongolian-Trans-Baikaliya) occurred in opposite directions. Thus, in the steppes of northern Kazakhstan, from the place of their summer residence, for example
712 Akmolinsk district and the Barabin steppes, kulan migrated in August into Bet-Pak-Dala in the eighteenth and nineteenth centuries. Some troops formed significant herds and moved southward in large congregations of some thousands of animals (Bikhner [Büchner], 1905). With the commencement of thawing of snow, kulan set off in a reverse migration and in April appeared again at their summer pastures. Some kulan migrated south even from northern Balkhash and the Ili valley beyond the Chu River (Nikol'skii, 1887). These migrations were motivated by the formation of a thick snow cover in the above northern regions.

A contrary phenomenon was observed in the eastern part of the range. In Mongolia, as a result of autumn impoverishment of pastures and snowfalls in the semi-deserts, kulan migrated mainly north into the steppe regions of eastern Mongolia and Barga as far as Trans-Baikaliya (Pallas, 1771; Radde, 1862; Cherkasov, 1867; Vinkler and Sabler, 1898*). Northward migrations into the steppe regions were determined by the presence of more abundant winter pastures in the herbage steppes and a much thinner snow cover than

---

*Not in Literature Cited—Sci. Ed.



711 Fig. 243. Basin of Lake Er-oilan-duz in Badkhiz (southern Turkmenia). Place of winter congregation of kulan, especially during snow and cold. Salt flats (white) visible. June, 1948 (see also Fig. 214). Photograph by V.G. Heptner.

in semideserts. Now, as a result of past migrations, regular transgressions of kulan are seen in the steppes of eastern Mongolia and rare intrusions into Trans-Baikaliya as well in the autumn–winter period (Bannikov, 1954). Southward migrations of kulan into Mongolia are not in the form of regular migrations but represent an insignificant displacement of kulan troops into regions or sections with less deep snow and more abundant nonsaltwort pastures. Only in years of exceptionally deep snow do mass migrations of animals into the southern regions of the Gobi take place. The same type of minor migrations are seen in the spring movements of kulan in Mongolia and China toward the Gobi Altai, eastern Tien Shan, and other uplands, on the slopes of which vegetation appears early because of a higher degree of moisture (Bannikov, 1959).

Reproduction. The reproduction of kulan has been studied very little and available information is fragmentary and often contradictory. In Kazakhstan kulan come into rut in June (Slovtsov, 1897). July–August are reportedly the most probable periods of estrus in Turkmenia according to Ishunin and Korovin (1945). In Trans-Baikaliya animals in estrus have been noted in September (Radde, 1862). In Mongolia symptoms of commencement of rut have been recorded for the last few days of June and July, but estrus extended

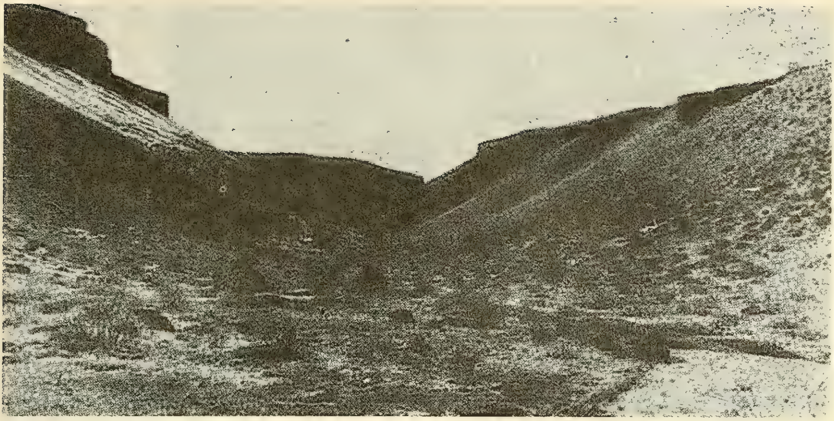


Fig. 244. Kyzyl-Dzhar gorge in Badkhiz preserve. Refuge of kulan in inclement weather. Photograph by A.O. Solomatin.

into August and early September (Bannikov, 1948). Evidently the periods of estrus are extremely protracted and variable, which is supported by the detection of foals of different ages in nature.

During the period of rut stallions "play". They make troops run round in circles while moving forward, and they lie on their back, roll, and neigh. During these playful interludes the young in the troop—yearlings and two-year-olds—invariably remove themselves 713 and watch the antics of adults from a distance. Stallions chase away any approaching male juvenile. According to Radde (1862) and Slovtsov (1897) during the period of rut severe combats occur and the hides of all the males caught showed marks of frequent battles; Radde reports innumerable scars. Males taking part in reproduction for the first time separate from the troop during the period of rut and wander extensively throughout the steppe in search of a mare or a troop with a young male at the head; they will stand for hours at the top of hillocks surveying rivals and are constantly ready for a fight (Radde, 1862).

The gestation period is not less than 11 months and foaling takes place between April and June inclusively. The appearance of young is seen in the Badkhiz from the end of April to June (Shcherbina, 1951) and rarely later. In Kazakhstan Slovtsov (1897) detected foals in May. The first foals have been sighted in Mongolia in May and June. According to Ishunin and Korovin (1945), based on observations in a zoological park, February to May is the period of foaling. However, under natural conditions, February and March are relatively less probable. In the Badkhiz preserve in 1953 a foal was born

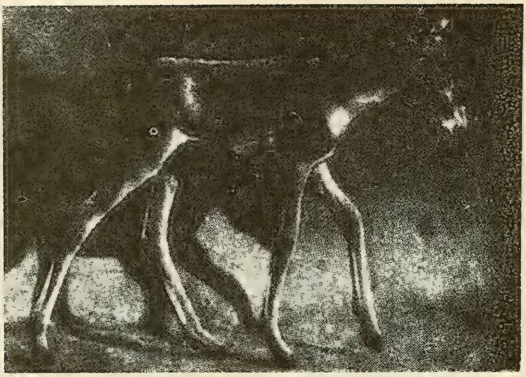


Fig. 245. Foal of Turkmenian kulan, 1.5 months old. Animal moving in amble. Nursery of Badkhiz preserve (southern Turkmenia). June, 1948. Photograph by V.G. Heptner.

on May 7, the mother of which had mated on May 23, 1952.[18] Usually a single foal is produced. Females begin to reproduce in nature in their second or third year; males commence breeding in their fourth year. In zoological parks males are capable of mating in their third year and females in their second. Information about the percentage of barren females is not available. Presumably females do not foal every year.

Growth, development, and molt. Within the first few hours of birth the newborn kulan is capable of running but tires soon. Usually it lies under the protection of grass or low bushes, not accompanied by adults. The mother grazes with the troop close by and more rarely (evidently, young females) leaves the troop temporarily to stay around the newborn. In the first few days the foal hides in the event of danger, but at age 10 to 15 days emerges from its shelter to join the troop. It begins to accompany the troop regularly within a month or a little more after birth, when it lives almost exclusively on grass. Lactation continues for about a month but, in a nursery, foals continued to suckle up to 9 to 12 months (Bannikov, 1959). Information is not available about the size of newborn foals and the growth of juveniles. They attain adulthood around 1.5 years of age. Milk teeth are replaced by permanent ones by the fourth year. Adults weigh from 160 to 260 kg.

Molt in Turkmenian kulan (Ishunin and Korovin, 1945) occurs from mid-April to mid-June. In Mongolia molt occurs later and molting periods vary highly according to the sex and age of the

---

[18] Date of mating not reliable.

animal. Males are the first to molt. By the beginning of July almost all males have light, bright summer hair, differing distinctly from that of females. Females are partially molted by early July; summer hair is seen on their head, legs, and partly the neck and flanks, while the back still bears the old, light sandy, dirty winter hair. Females
714 sport a full summer coat only by mid-July. Young yearlings and two-year-olds molt at the end of June to early July, i.e., their molting periods are intermediate between that of adult males and females, the molt of yearlings being more protracted (Bannikov, 1948 and 1954).

Enemies, diseases, parasites, mortality, competitors, and population dynamics. The wolf should be regarded as the main enemy of kulan. However, even this predator inflicts far less damage on kulan than on other ungulates. In a troop the animals are hardly accessible to a wolf. Even a single female can actively and successfully protect her foal from a wolf. Nevertheless juveniles, particularly in severe winters, often fall prey to wolves.

The diseases suffered by kulan have not been studied; only the abundance of stomach botfly *Gastrophilus pecorum* parasitizing this species can be mentioned. Ice crust formation and deep snow of over 40 cm thick are highly fatal to kulan. The main reason for the extinction of kulan in Kazakhstan was the severe winters of 1879/80 and 1891/92, after which the animals disappeared altogether in the Ustyurt, around the Aral Sea, the lower course of the Sarysu, and at other places (Sludskii, 1953). For the same reason, in 1934 many kulans died in Turkmenia (Ishunin and Korovin, 1945). Similar instances are known in Mongolia also.

Domestic livestock and especially sheep are the most serious competitors of kulan for pasture. However, the effect of livestock is reflected most in keeping kulan away from water holes.

In 1954 juveniles in Badkhiz represented 14.2% of the total population; in 1955 they constituted 14.2% [*sic*] (Kravchenko and Shcherbina, 1959).

The life span of the animals in nature is extremely prolonged. Animals older than 10 to 12 years have been captured often. Longevity in captivity is doubled.

Field characteristics. The kulan is somewhat smaller than the horse, slender, stands on long legs, but with a heavy head and a tail resembling that of an ass. From a distance it is very difficult to distinguish it from Przewalski's horse. Apart from the tail, kulan are seen at a distance to differ from Przewalski's horse in the more extensive chestnuts on the front legs, perceptibly longer ears, and generally smaller overall size. The hoofprints of kulan are tiny and narrow.

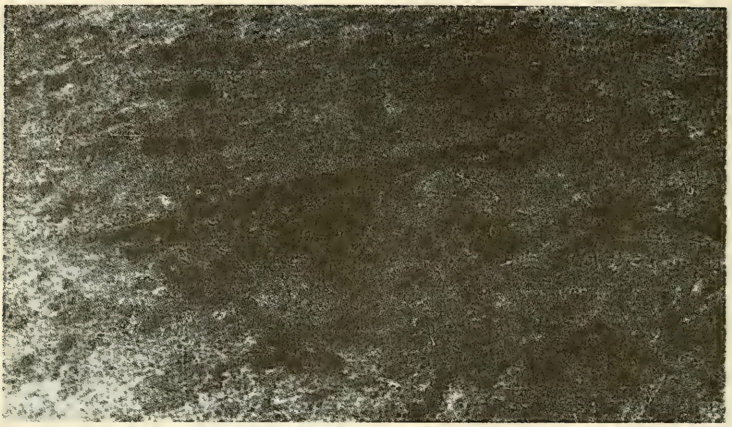


Fig. 246. Tracks of a troop of five or six kulan in a powdery solonchak in Kyzyl-Dzhar gorge in the Badkhiz (southern Turkmenia). Gun placed to show scale. June, 1948. Photograph by V.G. Heptner.

Well-beaten pathways and abundant feces, resembling those of domestic horse, are invariably seen around water holes. The kulan is a silent animal; its voice resembles the short shriek of an ass. (A.B.)

715 Economic Importance

Hunting kulan was strictly prohibited in the very first Soviet hunting laws (1919). Since 1941 much of the Badkhiz, covering an area of 800,000 hectares inhabited by this species in the Soviet Union, has been declared a preserve. The boundaries of this preserve were altered in 1951.

In the past kulan were hunted by lying in wait for them at water holes and by rounding them up. The latter method involved a group of hunters corraling a kulan troop in a circle. For this purpose more rugged country was selected, which provided good hiding places for the hunters. Numerical data on the number of animals caught annually are not available. In descriptions of hunts catches of three to five animals and sometimes more than ten in a single hunting expedition are often mentioned.

The meat of kulan is considered a delicacy and valued more than that of all other animals. In addition, the meat, and especially the fat, is thought to possess curative properties. The hide is also greatly valued. That from the abdomen of a female was used for making winter clothes and valuable Moroccan leather prepared for shoes and saddle trimmings.

Kulan survive well in captivity. Foals are usually caught at the age of three to five days. It is difficult to ensure that they do not break their legs during capture. Foals readily adapt to captivity and feed well. In zoological parks young kulan are fed cow's milk made slightly saline and diluted with water in the ratio of 1:3. Juveniles as well as adults are fed oats and hay. Many adult kulans die during attempted capture.

Innumerable instances are known of reproduction in captivity. Results of experiments on domestication are contradictory, however. There are references to domestication of kulan in the Middle East prior to that of horse, and their being used to draw chariots (Antonius, 1936). In the Badkhiz sanctuary kulan have been trained to draw droshkies [4 wheeled carriage] and have also been saddled (Klyushkin, 1950). Attempts elsewhere to saddle or harness kulan have not succeeded.

Numerous experiments on hybridization of kulan with ass and domestic horse have been successful (Ishunin and Korovin, 1945). In the Uzbek Soviet Socialist Republic hybrids have been obtained for several years from a male kulan and female ass or mare. These hybrids were exhibited in VSKhV [exhibition grounds in Moscow] in 1940. A hybrid of horse and kulan has a short mane and no forelock or chestnuts on the rear legs. The long hair of the tail grows only from the middle of the tail stump. The dark-colored stripe along the back and tail is fairly well-manifested. Hybrids of kulan with horse and ass have all proved nonfertile (Shchekin and Shkurgin, 1950). Instances are not rare of kulan mating in nature with Mongolian horse. Outwardly these hybrids are similar to kulan but have a fairly long mane and the tail stump has long hair over much of its length (Bannikov, 1948).

In 1953 seven kulan were released in a preserve on Barsa-Kel'mes Island for purposes of acclimatization (Sludskii and Strautman, 1955). They are also held under semidomestic park conditions in Askaniya-Nova. Live animals are highly valued in international trade. The scientific, aesthetic, and practical importance of kulan is very great. (A.B.)

2. TARPAN[19]

Equus (Equus) przewalskii **Poljakov, 1881**

1758. *Equus caballus.* Linnaeus. *Syst. Naturae,* 10th ed., p. 73. 716 Southern Sweden (domestic horse).

---

[19] This name is usually applied to wild horses of the European steppes of the

1828. *Equus sylvestris.* de Brinken. *Mémoire déscriptif sur la forêt Imperiale de Bialovieza en Lithuanie.* Varsovie. Belovezh Forest. Nomen nudum?

1881. *Equus przewalskii.* I.S. Polyakov. *Izvestiya Imp. Russk. Geogr. Obshch.,* vol. 17, p. 1, tabs. 1 and 2. Khanobo (Kanabo) sands about 250 km southeast of Zaisan post (roughly 46° N lat. south of Lake Ulyungur); central Dzhungaria.

1912. *Equus gmelini.* Antonius. *Naturwiss. Wochenschrift,* vol. 27, no. 33, p. 516. Zagradov steppe on the right bank of Dneper in its lowermost courses, near Kherson.

1920. *Equus gmelini* Ant. subspecies *silvatica.* Vetulani. *Bull. Intern. de l'Ac. des Sc. et des Lettres,* ser. B, no. 7B, 1927, p. 857. Belovezh Forest.

1951. *Equus tarpan.* Pidoplichko. *O lednikovom periode* (The Glacial Period), vol. 2, p. 233. Nomen nudum.

1811. *Equus ferus.* Pallas. *Zoographia Rosso-Asiatica* (Zoography of Asiatic Russia). Auctorum. Errorim![20]

1811. *Equus equiferus.* Pallas. *Zoographia Rosso-Asiatica.* Auctorum. Errorim![20] (V.H.)

In spite of the references of several authors and naturalists of the Ancient and Middle Ages, and recent travelers, the existence of true wild horses in the last century in Europe and western Asia was sometimes questioned. It was thought that the southern Russian tarpan and certain other forms of horses simply represented domestic animals turned feral. This was even asserted of the wild horses of Mongolia and Dzhungaria (Przewalski's horse).[21]

Soviet Union, i.e., to tarpan proper (form *gmelini*) but there is ample justification for extending it to the species as a whole.

The interpretation of the scope and structure of the species adopted here differs from that usually recognized, including some contemporary zoologists. For a justification of this viewpoint, an analysis and proof of several related aspects, and also establishment of synonyms, nomenclature, and type localities—see Heptner, 1955.

[20] The introduction into nomenclature of this name and the next with a reference to *Zoographia* by Pallas (Antonius, 1912; Lydekker, 1916; and others) as the oldest names of wild horses is based on some misunderstanding. In Pallas' works on horses these names do not occur at all. Pallas in *Zoographia* used the term "Equiferus" or "Equiferi," but invariably as a single word and in a purely descriptive and not nomenclatural context (see sections on horses and kulans in *Zoographia*).

[21] Domestic horses, even pure-bred forms, readily turn wild. Such feral horses were sometimes very abundant; troops or even whole populations of them have existed at different times in different countries. In the Soviet Union small numbers of wild horses lived in the deserts on the right bank of the Murgab and on Agrakhan spit (peninsula) on the western bank of the Caspian Sea (Heptner, 1955). Large troops of so-called mustangs once lived in the steppes of North and South America, while wild horses are seen even now in Europe in the Gascogne and Camargue. None of these horses is related to the tarpan. Feralization does not impart a tarpan-like resemblance.

Over a period of seventy to eighty years, and even partly in the last decade, enough data and material have been gathered which permit one to assert that true wild horses did survive in some parts of Europe and western Asia in the historic period and at some places even in the seventeenth, eighteenth, and nineteenth centuries. These animals, especially in the last century, sometimes hybridized with domestic horses. At some places hybridization was apparently reflected in their external appearance. However, the wild nature of tarpan as a species, irrespective of the pure bloodedness or lack of it, cannot now be disputed (Köppen, 1896; Heptner, 1955). In spite of the near total absence of museum material on tarpans of Europe and western Asia (osteological material is available for only two individuals), the outward appearance and other features of this animal are not difficult to conjecture. (V.H.)

Diagnosis

Large-sized animals. Tail covered with long hair throughout its length, commencing from base or only slightly short of it. Color dark gray (mouse) or yellow (roan) with dark-colored stripe on back; transverse bands in scapular area absent. Ears short. Auditory meatus short and not visible when skull viewed from dorsal side. (V.H.)

717

Description

In outward appearance the tarpan is a wholly typical horse: build compact and stocky, chest broad, back straight, ribs steep, and rear straight. Head large and heavy, muzzle short, and lower jaw posteriorly broadened; forehead straight or slightly concave, rarely slightly convex; ears small and upright; nostrils broad; and orbital section fairly broad. Neck short and thick. Shoulders (i.e., shoulder blades and humerus) highly developed and straight. Legs thin and strong, with small high hooves. Chestnuts on front legs invariably present but usually weakly developed; often absent on rear legs. Tail, compared to that of domestic horses, relatively short and less hairy; section of tail stump covered with short hair relatively large; sometimes tail fairly long. Mane short and erect; forelock absent; elongated hair on withers absent; long dense hairs present on rear of lower jaw.

General color yellow or rusty-yellow, more light-colored (whitish) or gray along lower surface, much lighter downward, and sometimes a fairly uniform gray. Mane and tail wholly black or blackish-brown or lateral hair of mane same color as neck. Legs below knee black or blackish-brown. Sometimes (in some light-colored animals) only hooves dark; sometimes faint, very dark-colored band seen against dark background of forelegs. Unbroken black, blackish-brown, or rusty-brown stripe extends down middle of back, from mane to the tail; sometimes stripe discontinuous and seen only on rear of body (croup) or even absent (rarely). Tip of muzzle light (white), or slightly lighter than rest of head, or the same color as head.[22]

Summer hair short and close-fitting, while winter hair fairly long, dense, and sometimes even curly on the back.[23] Winter coat a dirtier color than summer coat. Apparently the opposite occurs in some cases, with the winter coat being lighter, sometimes ashen, and even almost white exceptionally. Foals are similar to adults in coloration or (in dark gray tarpan) dark gray with a rusty tinge. Older animals are apparently somewhat lighter in color than juveniles.

In size tarpan are smaller than domestic horses of small breeds or equal to them. Height at withers 115 to 146 cm and basal skull length 445 to 495 mm.

In general build and appearance the tarpan is a handsome, strong, mobile, and energetic wild animal; its vision is "quick and lively", the eyes even "fiery". It is very high-strung and vicious when frightened. Attempts at domestication or captivity met with no success.

The above description applies to the typical tarpan of eastern (Central Asiatic) and western forms. On a level with the western (Kazakh and European) tarpan there occur some variant forms. The characteristics of some, at least in the last century, are associated with some admixture of the blood of domestic horses. In the western tarpan (west of Volga) this is reflected in some insignificant color differences,[24] lengthening of tail and its transformation into a dense structure, lengthening and transformation of mane into a short, hanging structure, and the presence of a fairly long forelock.[25]

---

[22] Tarpan are thus roan, light bay, or dark gray in color, and have been recognized as such by most older writers. These color types are geographically quite well separated (see below).

[23] In southern Russian steppe tarpan the hair was " . . . very long and so dense that, to the touch, it felt more like fur than horse hair" (S. Gmelin, 1771).

[24] Sometimes even ash-colored individuals have been observed in herds. These evidently represent stray domestic mares. However, some references to such tarpan are simply erroneous (Falz-Fain, 1919). In general, it should be emphasized that we have exaggerated views on the admixture of blood of domestic horses in that of tarpan. In fact, such admixture has been very insignificant, if indeed it has occurred at all. The reverse phenomenon, i.e., the effect of tarpan on local breeds of domestic horses, could at places be notable. For details, see Heptner, 1955.

718 The color of steppe tarpans, at least of southern Russian animals, even in the last century was very specific and stable.[26] Evidently, mane characteristics are most variable (its elongation and the appearance of forelock). (V.H.)

Taxonomy

All species in the genus *Equus* are closely related. Nevertheless, African forms reveal more primitive features (zebras—subgenera *Hippotigris* and *Dólichohippus*), and true horses, i.e., subgenus *Equus* and tarpan in it (*E. przewalskii*), should be considered more progressive animals, differing greatly from ancestral forms. Kulan (*E. hemionus*) and subgenus *Asinus* (ass, *E. africanus*) occupy an intermediate position between these two groups, the kulan being closer to tarpan than to ass. (V.H.)

Geographic Distribution

The range (reconstructed) covers Europe except in the north; the steppes and partly forest-steppes of the European part of the USSR; forest-steppes, steppes, and semideserts of western Siberia, Kazakhstan, and Middle Asia; and the plains of Central Asia.

Geographic Range in the Soviet Union

The range in the Soviet Union covers steppe and semidesert regions

[25] Lengthening of the mane is insignificant. The semisuspended mane on both sides of the neck would reach only one-third of the thickness of the latter or less (Heptner, 1934). The forelock is not a special formation and represents only the foremost, forward hanging portion of an elongated mane. The formation of the forelock and lengthening of the mane invariably occur as parallel developments. This has been noticed only in the southern Russian tarpan (*gmelini*); the mane of Dzhungarian tarpan (*przewalskii*) is erect.

[26] There are references (only one original, that of Gmelin) indicating that sometimes the ears are slightly longer and droop. The dubiousness of this feature aside (see section on kulan), there is no justification to see in it the effects of hybridization of tarpan with kulan, as is sometimes suggested. All available information about kulan and tarpan runs against this concept and, moreover, the very occurrence of kulan in the southern Russian steppes, at least in the period for which the information on tarpan is available (eighteenth century), cannot be regarded as strictly proved. Another result of hybridization sometimes put forward is the occurrence of some light, yellow-colored tarpan among dark gray tarpans; the explanation for this phenomenon is different (see below).

Even forms which lived in the first decade of the present century exhibited fairly typical coloration (Heptner, 1934).

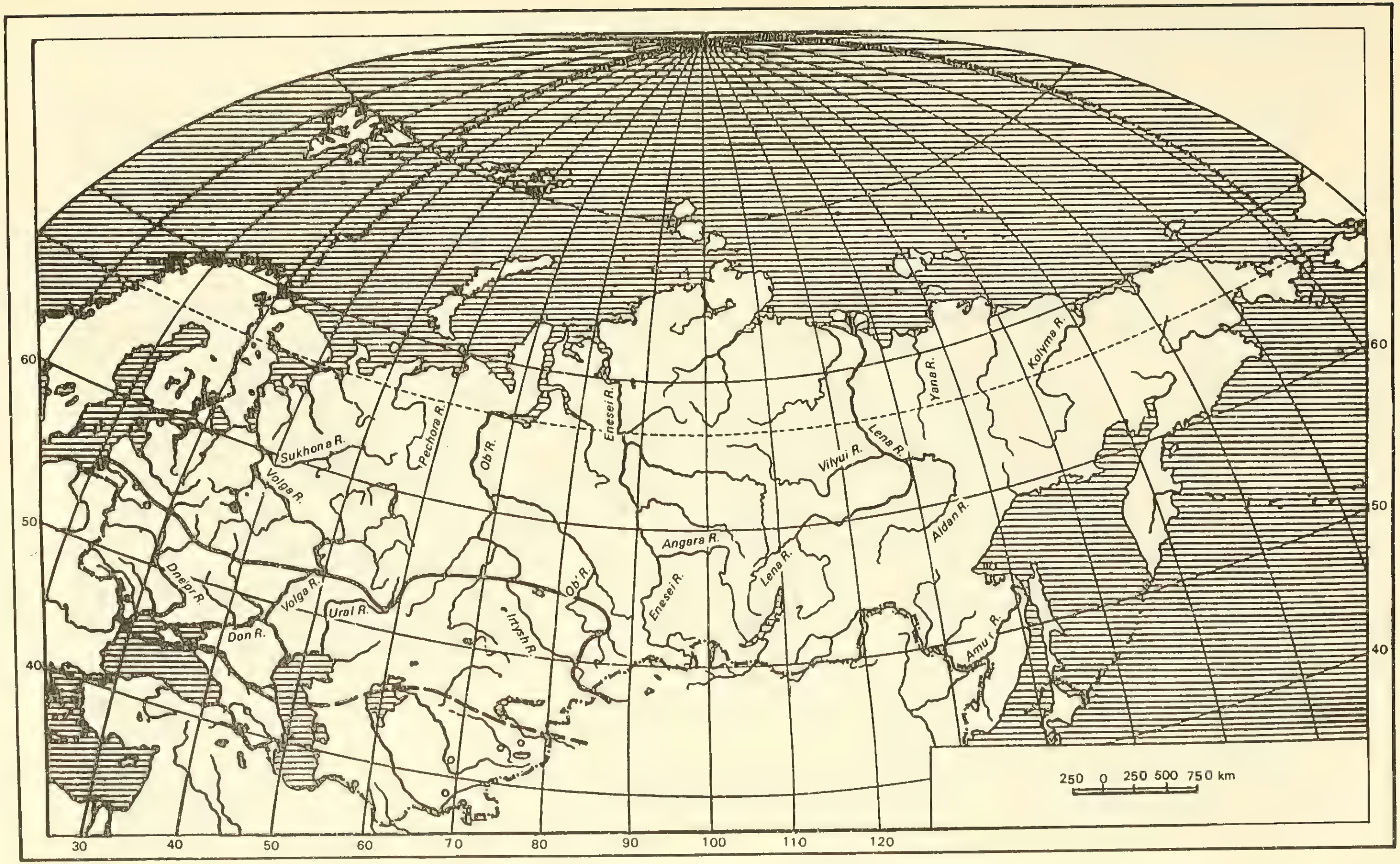
and a small part of the forest zone. Much of the range of the species, almost one-half, falls within USSR territory.

The range is divided into two unequally separated parts—Trans-Baikaliya and European Kazakhstan—which merge outside the USSR. At present tarpan are not found in the Soviet Union, not even stray animals.

In the European-Kazakhstan part of the range tarpan were very widely distributed in the historic period. In the northwest and west tarpan occurred in the forest zone of Lithuania (in particular, Troki [Trakai] near Vil'nyus) and in Kaliningrad district (in Kaliningrad until the early nineteenth century), in Belorussia (evidently only in its western and southwestern parts, in Belovezh Forest until the end of the eighteenth century), on the plains of the northern Pri-Carpathians, in the region of the upper Dnestr, and farther north even in the upper reaches of the southern Bug (Bar to the west and Brastslav to the south of Vinnitsa until the eighteenth century). In the southwest they were encountered in Moldavia beginning at the Prut (early eighteenth century). Farther east they occurred in the Black Sea steppes (to the 1860's), Crimean steppes (nineteenth century), Pri-Azov and Don steppes, Kuban and Pri-Kuma steppes (eighteenth and early nineteenth centuries), and apparently, in general, throughout the steppes of the Pri-Caucasus, in the steppes on the right bank of the lower Volga, and in the expanse between the lower courses of the Volga and Ural, in particular around the Ural estuary, and in the south to the Caspian Sea coast (early and mid-1800's).

Tarpan were present north to the longitudinal course of Ural (eighteenth century), along the Obshchii Syrtu (sources and upper
720 reaches of the Irtek River, a tributary of the Ural; sources and upper reaches of the Buzuluk, Karalyk, Irgiz, and Chagan Rivers), and northward to the city of Buzuluk, i.e., almost to the latitude of Kuibyshev (eighteenth century; Pallas, 1771 and 1773), along the Volga steppes, in particular at Saratov (mid-1800's), in the regions of Voronezh (Bobrov, eighteenth century), in Chernigov (Ros' River) and Kiev districts, and generally on the Ukrainian steppes (eighteenth and nineteenth centuries).

In the north these animals thus occupied the forest-steppe on the right bank of the Dneper, evidently to the latitude of Kiev. Between the Dneper and Volga the boundary rose north through Voronezh to Kuibyshev, i.e., the range covered the southern forest-steppe zone. Beyond the Volga it descended somewhat south, bypassing the Ural mountain on the south. It is highly probable that in the expanse between the Ural and Dneper the northern boundary of the range


Sukhona R.
Pechora R.
Ob' R.
Enesei R.
Yana R.
Kolyma R.
Vilyui R.
Lena R.
Volga R.
Aldan R.
Angara R.
Dnepr R.
Volga R.
Ural R.
Ob' R.
Enesei R.
Lena R.
Irtysh R.
Don R.
Amur R.
60
50
40
60
50
40
30
40
50
60
70
80
90
100
110
120
250 0 250 500 750 km

719 Fig. 247. Reconstructed range of tarpan, *Equus* (*Equus*) *przewalskii* Pol., in the USSR. Probable southern boundary in Middle Asia shown by broken line. V.G. Heptner.

lay somewhat north of the above-named places and the animal occurred throughout the forest-steppe zone.

The distribution of tarpan has not been well traced for the Asiatic part of the USSR. It no doubt occurred throughout the steppes and part of the forest-steppes of modern Kazakhstan and the southernmost part of western Siberia, from the Ural to Barabin steppe and Cis-Altai steppes inclusively, reaching east there, evidently to the Salair territory and Novosibirsk, and probably extending somewhat more to the east. The northern boundary of the range in the above region is not clearly known, but evidently coincided fairly well with the northern boundary of the steppes and proceeded roughly along 55°, at places along 54°, and even 56° N lat.

Data on the southern boundary are almost nil. There is no doubt that tarpan lived around the Ural estuary to the east of the river, at Emba estuary, in the region adjoining the east coast of the Caspian Sea, and probably in Mangyshlak.[27] The animal occurred even in areas north of the Aral Sea. There is justification to suggest the occurrence of this species in the region between the northern extremity of the Aral Sea and [Lake] Balkhash.

In the east tarpan were encountered east of Semipalatinsk (between it and Kolyvanya) and were extensively distributed in the easternmost part of present Kazakhstan ("Zyungor steppe"[28]—eighteenth century), and evidently also in the Zaisan depression.[29]

In southern Kazakhstan and the Middle Asiatic republics tarpan were either absent or became extinct so long ago that no information exists about their presence there.

The Trans-Baikal section of tarpan habitation covered the Daurian steppes in the Onon and Argun river basins. There, the animal survived evidently throughout the eighteenth century.[30]

---

[27] Information provided by S. Gmelin about this is not very reliable. However, he mentions their occurrence at "Tyuk-Karagan," probably having in mind Tyub-Karagan Cape, representing the westernmost extremity of Mangyshlak.

[28] As "Dzyungoriei", "Zyungoriei", "Dzyungor steppe", etc., Russian authors and geographers of the eighteenth century (for example, Tychkov, 1762) understood Semirech'e plains and part of northern Pri-Balkhash and adjoining places in the west even to Sarysu, and the region of Tarbagatai and Zaisan, excluding present-day Chinese Dzhungaria.

[29] There is a reference (Sedel'nikov, 1910; cited by E. Strautman, 1953) that Dzhungarian tarpan (Przewalski's horse) found their way into Chernyi Irtysh valley even at the beginning of the present century.

[30] The range of tarpan, unless otherwise stated, is based on Köppen, 1896; Anuchin, 1896; Heptner, 1955; Kirikov, 1955; and other sources and material cited by S.V. Kirikov.

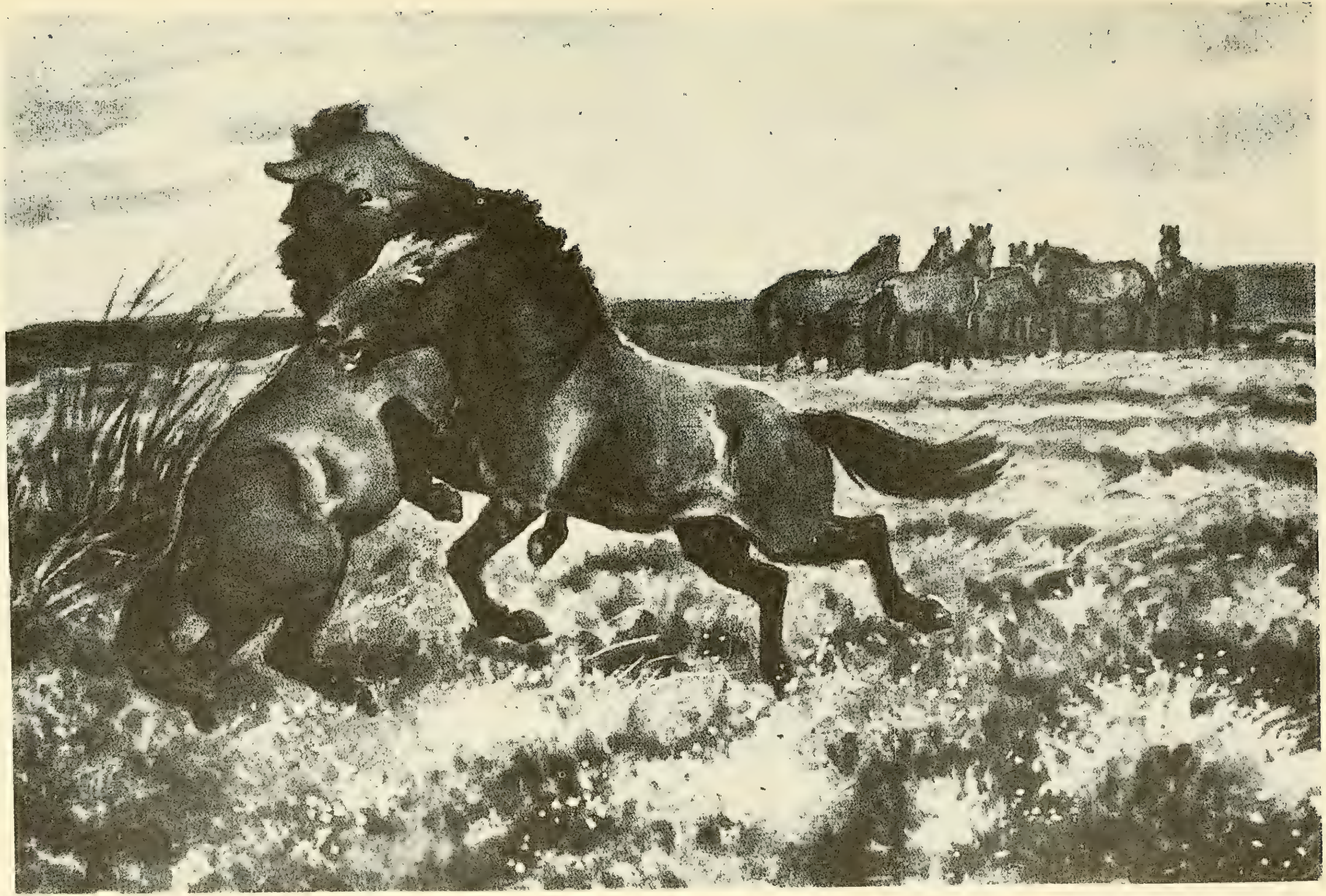


Plate 6. Tarpan, *Equus* (*Equus*) *przewalskii* Pol. Painting by A.N. Komarov.

Geographic Range outside the Soviet Union

Outside the Soviet Union tarpan were quite common over much of western Europe. Commencing from ancient times up to the nineteenth century one finds mention of their presence in Poland, several regions of Germany, including East Germany, Denmark and the Danish islands, Belgium, France, the Iberian Peninsula, Switzerland, and several other countries.

In the east the former range of tarpan in Central Asia is very poorly known. It covered all of Dzhungaria, evidently the whole of Mongolia (Inner Mongolia and Mongolian Republic, except the hills) and Kashgaria, at least its eastern parts.[31] Long ago, distribution in this region shrank drastically. In the last century horses were
721 quite extensively distributed in Dzhungaria, western parts of Mongolia, and adjoining Chinese regions. However, they did not extend to the Hwang Ho (not east of 105°30′ E long.). At present tarpan are still sighted in small numbers in the extreme southwestern parts of the Mongolian Republic (in Trans-Altai Gobi) and adjoining Chinese areas.

Judging from Assyrian bas reliefs (some seventh cent., B.C. [*sic*]; Heck, 1930; Rumyantsev, 1936; and others), wild horses were present in southwestern Asia, particularly in Mesopotamia. What they looked like and how their distribution related to the above-described areas are not known. In the prehistoric period (probably even in the period close to the present), tarpan survived in the British Isles and in northwestern Africa.[32] (V.H.)

Geographic Variation

A widely prevalent view holds that the European steppe and forest tarpan (forms *gmelini* and *silvatica*) and the Dzhungarian tarpan or Przewalski's horse (form *przewalskii*) represent different species. The former was usually given the name *caballus* or *gmelini*, sometimes *ferus*, and the latter *przewalskii*. Thus European wild horses

[31] Information about their occurrence in Kukunor and Tsaidam is erroneous.

[32] Foreign literature contains information (Harper, 1945; and others) about wild horses living in the Kolyma basin (along Omolon and Anyuy) even at the beginning of the present century. This information is based on a report by Pfizenmayer (1939), who took part in the excavations of the Berezov mammoth. No new positive information whatsoever about these "Lamuts wild horses (*Equus* sp.)" has been adduced since that time (1901) and it is clear that the source for this observation was some misunderstanding or relates to data on feralized horses. It should be pointed out that present-day Yakutian horses are very similar to tarpan. Finds of fossilized horse bodies are known from Siberia (Bunge's expedition).

were considered members of the same species as domestic horse and Przewalski's horse separated from them insofar as taxonomy is concerned. This view has been endorsed by some authors of recent monographs (Gromova, 1949). At the same time, as early as 1916 (Lydekker), it has been suggested that the Central Asiatic form be regarded only as a subspecies of *E. caballus.* New arguments have more recently been published in support of combining European and Asiatic wild horses in a common species (Heptner, 1955). The species name of this group should be *Equus przewalskii* Poljakov, 1881 (see footnote No. 17 on p. 540 and Heptner, 1955). This is the prevailing viewpoint among Soviet taxonomists.

Three subspecies of wild horses may be recognized under the species *E. przewalskii.*

1. Southern Russian steppe tarpan, *E. p. gmelini* Antonius, 1912.

Relatively large-sized. Color dark gray, with a black mane and tail, and invariably with a well-developed, fairly extensive, black stripe down the entire back (from mane to tail stump). Lower half of legs (up to knee joint) black. Color of young rust-tinged. Winter coat long and dense, slightly wavy along the back, and dirtier looking than summer coat; evidently, some fading of color occurs in winter (ash color results). Facial part ("muzzle") of skull relatively short, molar teeth relatively small, and frontal profile slightly concave.

Found in the steppes and forest-steppes of the European part of the USSR from the Prut in the east roughly to the Ural River, and probably to the Volga (see below).

Occurrence outside the USSR not known. Possibly occurred farther west (Rumania). However, it is not possible just now to reconstruct which form or forms of tarpan lived in central and western Europe. Probably steppe tarpan had a smaller distribution in the west and those living there were more likely members of the following subspecies (see below).

This subspecies became totally extinct in the eighteenth and nineteenth centuries. The last of these animals survived (often in captivity) up to the 1870's and 1880's and the very last of them on a stud farm as late as 1914 to 1918 (Heptner, 1934).[33] Attempts have been made to "reconstruct" this form. The general appearance of the animal has been reproduced rather well but genetically this form has nothing in common with the true steppe tarpan (see later).

---

[33] The so-called "Shatilov tarpan" caught in the steppes close to Kherson in 1866, which lived in Moscow Zoological Garden as late as the 1880's, is usually considered the last of the free tarpans. Actually, the last animal was a mare killed at the end of December, 1879 in the Tavrichesk steppe at a place called "Agaimansk Pod" at Agaiman village, 35 km from Askaniya-Nova (Falz-Fein, 1919; Heptner, 1955).

2. Forest tarpan, *E. p. silvaticus* Vetulani, 1928 (an *sylvestris* de Brinken, 1828?).

This subspecies is very similar to the preceding one but slightly smaller and of a weaker build; also fading of color is more intense in winter.

Found in western and southwestern Belorussia, Lithuania, and adjoining territories.

Outside the USSR this tarpan survived in Poland, Germany, and evidently some other parts of western Europe.

This horse, unlike all other forms, survived mostly in the forest environment during the final phase of its existence, probably even in the large forest massifs of Poland, Lithuania, and the territory of former Prussia, where it survived the longest. Evidently this tarpan was displaced into large forests as a result of persecution by man. The forest tarpan, at least in the form in which it survived until the last century, could probably be considered a stunted form of steppe tarpan.

In central Europe the forest tarpan disappeared in the early Middle Ages or even earlier, while it survived in the east up to the sixteenth, seventeenth, and eighteenth centuries. The rest of the free-

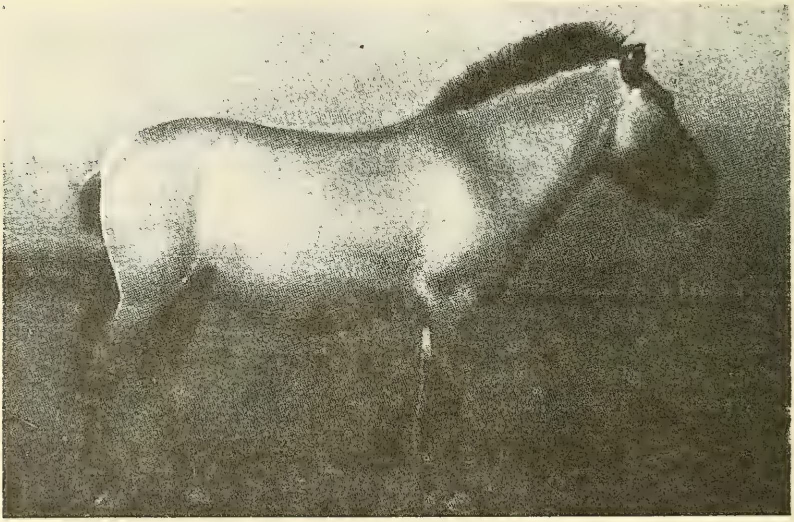


Fig. 248. Mare of Dzhungarian tarpan or Przewalski's horse, *Equus* (*Equus*) *przewalskii przewalskii* Pol., from Mongolia, "Orlitsa III" ("Altai"), living in Askaniya-Nova. Purebred animal caught in wild. Photograph by D. Kramarenko.

living forest tarpans survived until the end of the eighteenth century in Belovezh Forest. The last of them were killed at the beginning of the nineteenth century (1814—Kaliningrad district).

Attempts have been made to reconstruct this form which is genetically quite justified (see later).

3. Dzhungarian or eastern tarpan, Przewalski's horse, *E. p. przewalskii* Poljakov, 1881.

Larger than *E. p. gmelini,* general build heavier and unwieldy, head more massive and heavy, and neck thicker. Body length 220 to 723 280 cm; tail with hair 92 to 111 cm, without hair 38 to 60 cm; length of ears 14 to 18 cm; and height at withers 120 to 146 cm. Weight 200 to 300 kg. Basal length of skull 474 to 495 cm.

General color yellow with a rusty tinge, tip of muzzle whitish, and legs dark-colored (brown or black) up to knee joint, sometimes so only around hoof. Dark-colored stripe runs down back but poorly expressed and seen only in summer coat; stripe narrow, brown or rusty-brown, sometimes sparse and seen only on croup, and sometimes absent. Tail and mane black or blackish-brown. Mane from sides edged by some light colored hair, which is invariably short and erect. Forelock absent. Winter coat long and dense, on back slightly wavy, and lighter in color than summer coat.

Facial part of skull somewhat elongated, molars larger than in steppe tarpan, and skull profile straight or slightly concave, rarely convex.

Found in Kazakhstan westward to the Urals and western Siberia, possibly steppes east of the Volga, and Trans-Baikaliya. Outside the USSR found throughout the Central Asiatic part of the range of the species.

At present, within the Soviet Union, this tarpan is absent and almost extinct even in Central Asia. Only a small number of these animals live freely in the Trans-Altai Gobi in Mongolia and the adjoining expanses of western China. It is possible that a few individuals are still to be seen at other places in China.

Until recently it was thought that this form of wild horse did not occur within the Soviet Union (for example, E. Strautman, 1953) or only reached the USSR along the Chernyi Irtysh (Sedel'nikov, 1910). However, it has recently been shown (Heptner, 1955) that those wild horses which survived in Kazakhstan even in the eighteenth and part of the nineteenth centuries were of this form. There are indications to suggest that tarpan occurring on the Ural and even north of its longitudinal course had the color ("roan") of the Dzhungarian tarpan described above. However, even darker ones, i.e., "dark gray", were also sighted in that region (Rychkov, 1762).

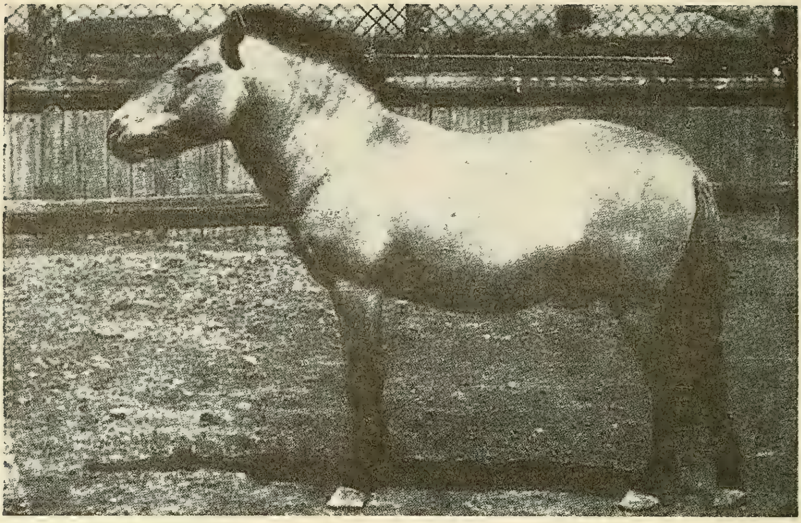


Fig. 249. Stallion of Dzhungarian tarpan or Przewalski's horse, *Equus* (*Equus*) *przewalskii przewalskii* Pol. Purebred stallion "Orlik" ("Robert") born in Munich Zoological Garden (Hellabrunn) in 1943. Photograph taken in October, 1958 by D. Kramarenko.

724 Information available for the first half of the nineteenth century, pertaining to the steppes east of the Volga at the latitude of Saratov and southward, reveals that tarpan of this region were "gray or sandy" in color (Eversmann, 1850). Evidently the area of intergradation ("transition zone") of the two races of tarpan, i.e., Dzhungarian and steppe tarpans, and where the ranges overlapped one another, was the steppes between the Volga and Ural, and directly adjacent to the Ural on the east. There is no doubt that hybrids also occurred there. It is also possible that a special form of tarpan, perhaps of hybrid origin, existed in this region.[34]

Outside the Soviet Union, on the mainland of Europe, tarpan did not occur, apart from the forest tarpan in Poland. At some places in France (Camargue in the estuary of the Rhone and Gascogne) some lone domestic horses which have turned feral may be seen. In Cornwall (Exmoor), England a small number of very primitive horses live freely and are known as Exmoor ponies. They are sometimes regarded as direct descendants of wild horses and even as a special race of this species (form *britannicus* Sanson, 1869). (V.H.)

---

[34] On the Obshchi Syrtu where tarpan extensively hybridized with domestic horses, animals of "brownish," "hazel," and "grayish-iron" shades were once known; black horses were very rare and skewbald animals absent (Pallas, 1773). Dal's dictionary may be consulted for color terminology.

Biology

Very little information exists on the biology of tarpan and the available material pertains mainly to the southern Russian tarpan.[35] The south Russian steppes provided a most suitable environment for the survival of tarpan when they were almost unpopulated. This vast region was covered with feather grass, sheep's fescue, and other steppe grasses, with areas supporting steppe shrubs (wild cherries and others). Small lakes with plentiful reed shoots and colonized by a large number of aquatic birds could be found throughout the steppes. Tarpan were confined around these lakes. They grazed in the steppes and used the lakes as water holes. In winter the animals dug up grass from under the snow. These large uninhabited expanses enabled tarpan to wander extensively during unfavorable conditions (drought, steppe fires, and ice crust formation).

In these years, i.e., roughly to the early part of the last century, tarpan were numerous and the activity of man did not seriously affect their life. The animals lived in troops, usually of 10 each and sometimes up to 15, under the leadership of a stallion. The stallion guided and defended his troop. Thus, on going to a water hole the male went ahead first, examined the site, and having made certain of safety, returned to the troop and led it forward. While grazing, the stallion often surveyed the steppes, usually from a mound. The leader took care of his troop and fought other stallions attempting to steal his mares. Severe combats between males were not uncommon. The animals were very agile and capable of sustained running. Even foals fell prey to hunters only after a long and persistent chase and it was almost impossible to catch an adult. The latter was seldom attempted in days gone by. Only occasionally were tarpan lassoed by hunters, using the best of horses and then too in groups or relays, and after a daylong chase. Usually newborn foals were caught after killing or driving away the mother. Tarpan were very cautious animals. They came quite close to a man on foot but ran away a few kilometers from one on horseback.

In olden times, in spring, during the period of rut, old males drove younger rivals out of the troops. The foals during this period lived in small groups or singly. Newborns still unable to move with the herd were usually thrown down on the steppe by the mother and bedded in dense grass in the event of danger.

Tarpan sometimes chased domestic mares, often after a fight with a stallion leading a domestic herd. This occurred at places near

---

[35] Only the most general information is given here.

725 horse ranches where horses roamed the steppes throughout the year, or much of it, without supervision. There were also instances when tarpan enticed mares away even from well-protected herds and even separated harnessed mares, thus posing some threat to the owners. An encounter with a tarpan male in the steppes by a rider, especially one on a mare, could sometimes pose serious danger.

The foregoing episodes took place during the last 50 to 100 years of the existence of southern Russian tarpan, when the population was already on the wane. Thereafter reclamation of the steppes proceeded rapidly and livestock husbandry developed quickly.

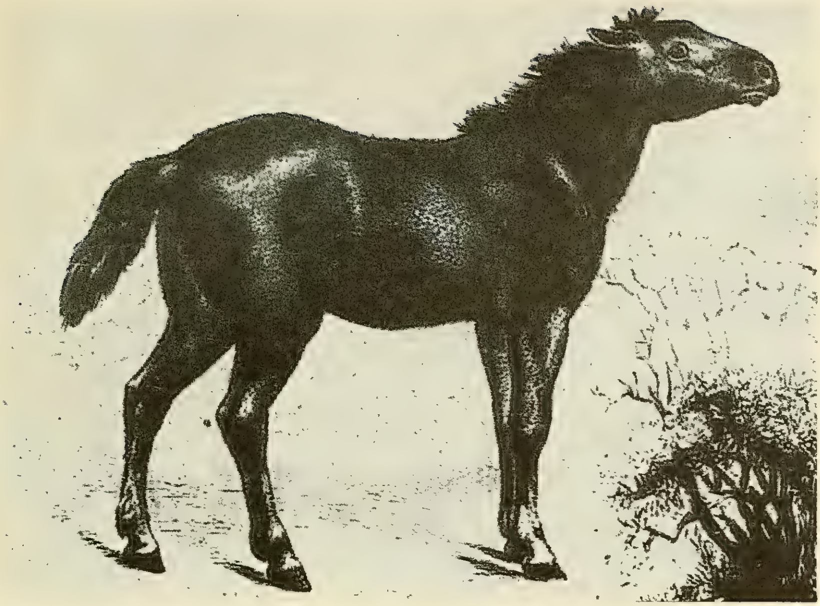
The habit of stealing mares resulted in the hybridization of tarpan with domestic horses and some believe that this intermixing occurred on a significant scale. Actually, however, it was not so extensive. This is supported by the high constancy of characters of south Russian tarpan until the very last days of its life. Moreover, not a single instance is known of a herd of wild horses led by a domestic stallion. Tarpan herds were invariably led by their own stallions. The presence of a small number of domestic mares could not perceptibly lower the pedigree of the population of wild horses (Heptner, 1955). Only in the last decade of their survival, when tarpan were few in number and formed small groups or roamed as solitary animals, could domestic stallions have mated with wild mares.[36]

On the other hand, mares in foal or mares with foals living in a troop of tarpan, sometimes returned to a troop of domestic horses and thus the blood of tarpan entered domestic horses. Wild stallions, especially the young, often mated with domestic mares, usually after a battle with the domestic stallion. At some places in the south domestic stallions were even shod on the hind legs to give them an advantage in a fight with tarpan. Sometimes captured tarpan were used as sires. The type of domestic horses seen in some localities, for example Kazakhstan, suggests that the admixture of the blood of tarpan occurred on larger scale than is customarily assumed (Heptner, 1955).

The stealing of horses, particularly in the Russian southern steppes, turned farmers against tarpan and they persistently chased them with the sole object of killing them. Another reason for violence against tarpan was that herds consumed hay stacked in the steppes. In winter tarpan herds would completely decimate haystacks. Cultivation of the steppes greatly interfered with the life of

---

[36] At places, for example on the Obshchi Syrtu, hybridization could have been more developed (see footnote no. 34 above).



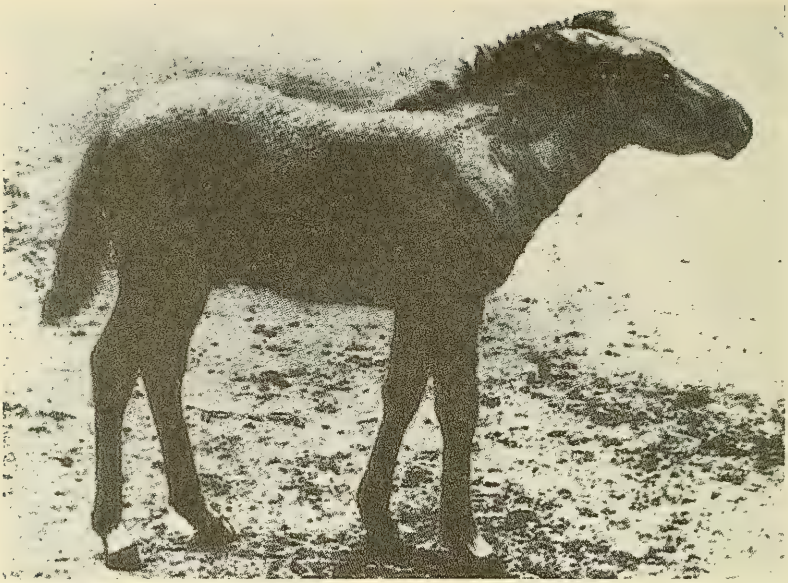
726 Fig. 250. Nineteenth century drawing of southern Russian tarpan (from Brehm, 1862).

these animals since it deprived them of their natural winter pasture and reduced their wanderings. The animals remained on all trails to haystacks, where ambushes were set up for them. A tarpan, frightened by one, would become stuck in the deep snow of ravines or gorges and fall into the hands of its persecutors. There is no doubt that tarpan did damage crops. But they were also hunted in the east for their meat and hide. Groups of hunters on horseback used to chase and spear them.

The drying of lakes which tarpan regularly visited during pasturing and the general deterioration of water holes also played a role. The animals were compelled to visit wells from which livestock drank and were shot there. Finally, the hunting of tarpan was considered a difficult and dangerous sport in which man could exhibit not only his bravery, but also test the quality of his horses.[37] Tarpan were given no respite anywhere. There is no doubt that tarpan were doomed to death by the economic advancement of the country, brought about by the rapid settlement and cultivation of the steppes in the nineteenth century, especially in the last of tarpan refuges, i.e.,

---

[37] See the colorful description of the death of the last mares living freely as given by Falz-Fein (1919) and partly by Heptner (1955).



726 Fig. 251. "Reconstructed" tarpan of Munchen Zoological Garden (Hellabrunn). Photograph by H. Heck.

the Tavrichek steppes, and after the Crimean War and the eviction
726 from there of the Nogaits [people]. However, direct persecution greatly hastened this process and destroyed the animal at a time when adequate areas of steppe expanses were still available to the species.

Severe winters also took a toll of tarpan. During excessively snowy and frosty winters, with shortages of fodder and frostbound soil conditions, the animals died en masse. In the past, when the animals were generally abundant, the population was restored relatively quickly. But during periods when the population was already small, losses became irretrievable and the process of extinction accelerated.

Instances are known of taming tarpan caught young and their use as riding horses.[38] There were also stray reports of taming tarpan caught as adults. In general, however, tarpan were vicious, wild, and indomitable animals. Because of difficulties in stabling them, using them, and the dangers they posed, captured adult tarpan were ultimately simply killed. Halfbreeds, commonly used as riding horses by herdsmen, were characterized by superior strength, endurance, speed, and fiery temper, although more tractable than wild tarpan. (V.H.)

---

[38] The so-called Statilov tarpan (Kherson) which died in Moscow Zoological Garden in the 1880's as well as the tarpan described by Heptner (1934) were used for riding.

Economic Importance

Tarpan as a species served as the ancestral stock for the evolution of domestic horse. Steppe and forest-steppe tarpan apparently played the main role in this process, but equally important were the Dzhungarian tarpan, which represent the parent stock of different groups of present-day breeds. Views of animal breeders about the role of different forms of wild horses vary, however, partly as a result of vague ideas of the taxonomy of wild horses. The domestication of 727 horses occurred in the remote prehistoric period but, as mentioned above, tarpan did exert some influence on present-day species even in the last century.

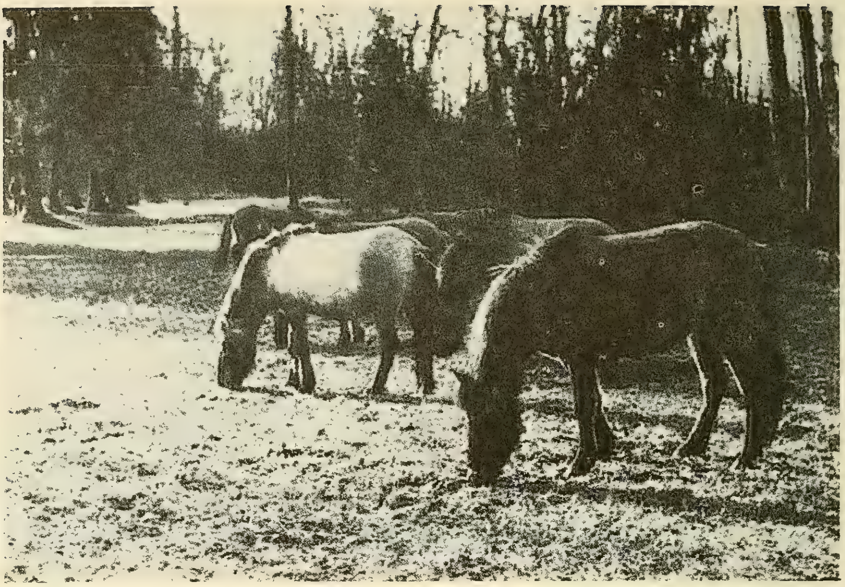
Tarpan exerted some adverse influence on the growth of agriculture and animal husbandry in the south and played a small role as a game animal.

With the extinction of steppe and forest tarpans, much of their scientific and aesthetic value has been irretrievably lost. Therefore attempts at "reconstructing" one or the other form to produce an animal outwardly resembling the wild European horse are understandable. The reconstruction of forest tarpan initiated by T. Vetulani[39] in Poland (Belovezh Forest) in the 1930's, began with the selection of the primitive Polish farm horse, which bears some features of forest tarpan, ("Polish konik"), and has proceeded to the building up of external and physiological characteristics.

Forest tarpan not only lived freely in Belovezh Forest in the eighteenth century, but were preserved in fairly large numbers up to the early nineteenth century in the Zamoisk animal nursery in Zamost'ya (between Kholm and Ravaya Russkaya). They also originated from Belovezh Forest. In 1808 all the animals were dispersed under the care of local farmers, who ultimately domesticated them and put them to work. In this region, even up to the early 1930's, the tarpan type was well preserved. Naturally some amount of genotype deviation was unavoidable after 120 to 130 years of domestication and free interbreeding with domestic horses. The most typical tarpan-like dark gray horses from the region of Zamost'ya, with dark legs, large head, and

---

[39] The procedure and results of this experiment, continued up to the 1950's, have been described by Vetulani in several publications. For a list of these works, see Vetulani, 1952.



728 Fig. 252. Group of "reconstructed" tarpans in Munich Zoological Garden (Hellabrunn). Photograph by H. Heck.

some other tarpan features have served as the base stock in experiments on tarpan "regeneration".

These experiments, in spite of loss (export to Germany) of a large part of the breeding stock during the War years, led to a fairly complete restoration of forest tarpan by the 1940's and early 1950's. In fact, these animals even at the end of the 1950's sported a fairly long mane, luxuriant tail, forelock, etc., but their general appearance was highly "tarpan-like", tending to form an erect mane, undergoing significant color fading in winter, and exhibiting other characteristics toward the evolution of a more complete tarpan type.

The animals live in total freedom in the forest, survive the winter without refuge, and are given additional food only in exceptional cases. These horses can be considered to some extent genetically related to tarpan and not just phenotypic copies in appearance.[40] These animals are not only useful as such, but also for hybridization purposes. There is no disputing their importance as farm animals.

---

[40] The experimental station of the Polish Academy of Sciences at Popeline in Olsztyn province has been conducting studies since 1955 on tarpan-like horses. Some of the horses are kept in natural surroundings, while others live under normal stall maintenance.

Almost simultaneous with these attempts at reconstructing tarpan, experiments (having in view apparently steppe tarpan) were initiated in central Europe in Berlin (L. Heck) and Munchen (H. Heck) Zoological Gardens. However, the method adopted in Germany differed: extensive hybridization was done using small-sized German farm horses similar to the Polish "konik"; the latter represents a form of pony, and Dzhungarian tarpan (Przewalski's horse). Just before the War a herd of these horses was released in Shorfheid Game Farm in central Europe.

The animals in the Berlin Zoological Garden died during World War II. They survived in Munich and at present several dozen are still living and have even acquired tarpan characteristics. In this case, however, no real genetic link with tarpan can be claimed. This is a special breed of very limited use, i.e., for exhibition in zoological gardens as a live ancestor of domestic horse. The purpose of raising this animal was only that and its value per se unquestionable.

Just a little over several tens of Dzhungarian tarpan still survive in Mongolia and China (see above). There is no doubt that, because
729 of its strength, endurance, and speed, this form has acquired great importance in horse husbandry. Its scientific and aesthetic value is very great. Unfortunately, however, measures suggested for the protection of Przewalski's horse are very difficult to implement and, in spite of a ban on hunting, this form is doomed to rapid extinction.

In various zoological gardens on January 1, 1958, there were 50 descendants of animals caught and brought to Europe even toward the end of the last and early part of the present century. The largest groups are found in Prague (12 animals), Catskills (USA—10 animals), Whipsnade (England—6 animals), Munich (7 animals), and some stray animals dispersed elsewhere (one to three each; Volf 1958). Evidently these should serve as a stock for conservation and further multiplication of Dzhungarian tarpan. In the Soviet Union there are only four animals (three in Askaniya-Nova and one in the zoological garden at Yerevan) and in Mongolia (Shargalantui) one living in captivity. By November 1, 1960 the total number of animals had increased to 73 (Z. Veselovskii). In 1958 an international project was initiated for the protection of Przewalski's horse, similar to project proposed for the conservation of wisent. (V.H.)

Literature Cited*

730–758 The references listed below include only works cited in the text**. Works cited under the synonymy of various species and groups have not been included.

Works used in any manner for writing this book and not mentioned in the text, save for a few exceptions, are also not included in this list. In other words, this list of references is not to be considered a comprehensive catalog of works on ungulates of the Soviet Union.

Abduldabekov, K.V. 1949. Okhotnich'i i promyslovye zhivotnye zapadnoi chasti Talasskogo Alatau (Hunting and game animals of western Talas Alatau). Kand. Diss.

Abramov, K.G. 1928. Pyatnistyi olen' (Sika). Vladivostok.

Abramov, K.G. 1929. Nekotorye dannye o pyatnistom olene (*Cervus hortulorum* Sw.) v Primor'e [Information on sika (*Cervus hortulorum* Sw.) in Primor'e]. *Zap. Vladivost. Otd. Russk. Geograf. Ob-va,* vol. 2, no. 19.

Abramov, K.G. 1930. Pyatnistyi olen'. Elementarnye svedeniya po pantovomu olenevodstvu (Sika. General information on reindeer breeding for antlers in velvet). Vladivostok.

Abramov, K.G. 1939. Amurskii goral (Amur goral). *Nauch.-Metod. Zap. Gl. Upr. po Zapovedn.,* no. 44.

Abramov, K.G. 1939. Zakonomernosti rasprostraneniya pyatnistogo olenya v predelakh Primorskogo kraya (Distribution pattern of sika within Primor'e region). *Nauch.-Metod. Zap. Gl. Upr. po Zapovedn.,* no. 3.

Abramov, K.G. 1949. Materialy k rasprostraneniyu, ekologii i promyslu losei Priamur'ya (Data on distribution, ecology, and hunting of Priamur elk). *Byull. Mosk. Ob-va Ispyt. Prirody Otd. Biol.,* vol. 54, no. 1.

Abramov, K.G. 1954. Kopytnye zveri Dal'nego Vostoka (Ungulates of the Far East). Khabarovsk.

Adlerberg, G.P. 1931. Antilopy Severnogo Tibeta i sopredel'nykh

---

*Some references are incomplete in Russian original—General Editor.

**As noted above, not all text citations appear here. The order of citations also differs from that of the Russian text, having been rearranged to conform with the Latin alphabet—Scientific Editor.

rainov (Antelopes of northern Tibet and adjoining regions). *Dokl. AN SSSR.*

Adlerberg, G.P. 1932. Critical review of genera *Nemorhaedus* H. Smith and *capricornis* Ogilby. *Izv. An SSSR, Otd. Mat. i Est. Nauk.* Leningrad.

Adol'f, T.A. 1948. Izmeneniya rasprostraneniya saigi (Variations in the distribution of saiga). *Okhrana Prirody,* no. 2.

Adol'f, T.A. 1950. Saiga v astrakhanskikh stepyakh pravoberezh'ya Volgi (Saiga in Astrakhan' steppes on the right bank of Volga). *Okhrana Prirody,* no. 10.

Adol'f, T.A. 1954. Nekotorye dannye po biologii saigaka v Astrakhanskikh stepyakh (Some data on the biology of saiga in Astrakhan' steppes). *Uch. Zap. Mosk. Gos. In-ta im. V.P. Potemkina,* vol. 28, Zool., no. 2.

Adol'f, T.A. 1957. Dinamika areala i chislennosti saigi (Geographic distribution and population dynamics of saiga). *Okhrana Prirody i Zapovednoe Delo v SSSR, Byull.,* no. 3.

Afanas'ev, A.V. and A.A. Sludskii. 1947. Materialy po mlekopitayushchim i ptitsam Tsentral'nogo Kazakhstana (Data on mammals and birds of central Kazakhstan). *Izv. AN Kazakhsk. SSR,* no. 36.

Afanas'ev, A.V., V.S. Bazhanov, M.N. Korelov, A.A. Sludskii and E.I. Strautman. 1953. Zveri Kazakhstana (Animals of Kazakhstan). Alma-Ata.

Aharoni, J. 1930. Die Säugetiere Palästinas. *Zeitschr. f. Säugetierk.,* vol. 5. Berlin.

Akhmedzhin-Abdul-Gallyamov-Abdiev. 1858. Kirgizskaya okhota na saigakov (Saiga hunting in Kirgizia). *Lesovodstvo i Okhota,* no. 47.

Alekperova, N.A. 1955. Iskopaemaya binagadinskaya saiga. Binagadinskoe mestonakhozhdenie chetvertichnoi fauny i flory (Binagadin Saiga Fossils. Binagadin Finds of Quaternary Fauna and Flora). Baku, pt. 4.

Aleksandrov, V.N. 1958. K izucheniyu estestvennogo pitaniya zubrov v Kavkazskom zapovednike (Study of the natural food of bisons in Caucasian preserve). *Tr.Kavkazsk.Gos. Zapovedn.,* no. 4. Maikop.

Aleksandrova, I.V. 1957. Materialy po chislennosti losei v Priokskо-Terrasnom zapovednike i v Moskovskoi oblasti (Data on elk population in Priok-Terras preserve and in Moscow district). *Tr. Prioksko-Terrasn. Gos. Zapovedn.,* vol. 1.

Aleksandrova, I.V. 1957. Opyt otpugivaniya losya ot molodykh sosnyakov (Experience in driving away elk from young pine plantations). *Tr. Prioksko-Terrasn. Gos. Zapovedn.,* vol. 1.

Aleksandrova, I.V. and L.I. Krasovskii. 1957. Nablyudeniya na letnim pitaniem losya v Prioksko-Terrasnom zapovednike (Observations on summer food of elk in Priok-Terras preserve). *Tr. Prioksko-Terrasn. Gos. Zapovedn.,* vol. 1.

Aleksandrova, V.D. 1935. Letnii korm olenei na Gusino Zemle (Novaya Zemlya) [Summer food of deer in Gusinyy Land (Novaya Zemlya)]. *Tr. Arktichesk. In-ta,* vol. 22.

Aleksandrova, V.D. 1937. O zimnem pitanii domashnego olenya na Novoi Zemle (Winter food of domestic deer in Novaya Zemlya). *Sov. Olenevodstvo,* no. 9.

Aleksandrova, V.D. 1940. Kormovaya kharakteristika rastenii Krainego Severa (Food value of plants of the Far North). *Tr. N.-I. In-ta Polyarn. Zemledeliya, Ser. Olenevodstvo,* no. 11.

Alekseenko, I. 1958. Poyavilis' los' i kozy (Elk and goats sighted). *Okhota i Okhot. Khoz.,* no. 2.

Allen, G.M. 1939. A checklist of African mammals. *Bull. Mus. Comp. Zool.,* vol. 83. Harvard, Cambridge, Mass., USA.

Allen, G.M. 1940. *Mammals of China and Mongolia,* vol. 2. *Natural History of Central Asia,* vol. 2, pt. 2. New York.

Anderson, R.M. 1946. Catalogue of Canadian recent mammals. *Nat. Mus. Canada, Bull.,* no. 102, *Biol. Series,* no. 31.

Andreev, P.N. and K.P. Andreev. 1948. Infektsionnye bolezni svinei (Infectious Diseases in Swine). Moscow, 4th ed.

Andrews, R.C. 1924. Living animals of the Gobi desert. *Nat. Hist.,* no. 24.

Andrushko, A.M. 1955. Mlekopitayushchie vysokogornoi doliny Alai (Pamir) [Mammals of the montane Alai valley (Pamir)]. *Uch. Zap. Leningr. Gos. Un-ta,* no. 181, *Ser. Biol. Nauk.,* no. 38.

Anon. 1891. Borzhomskii zverinyi otvod (Borzhomi Animal Farm). St. Petersburg.

Anthony, H.E. 1928. *Field Book of North American Mammals.* New York-London.

Antipin, V.M. 1941. Mlekopitayushchie Kazakhstana. T. 3, Kopytnye (Mammals of Kazakhstan. Volume 3, Ungulates). Alma-Ata.

Antipin, V.M. 1946. K ekologii dikogo gornogo kozla (*Capra sibirica*) [Ecology of wild Siberian ibex (*Capra sibirica*)]. *Vestn. AN Kazakhsk. SSR,* no. 11 (20).

Antipin, V.M. 1946. Materialy k faune mlekopitayushchikh Tsentral'nogo Tyan'-Shanya (Data on mammalian fauna of central Tien Shan). *Vest. AN Kazakhsk. SSR,* nos. 7–8, pp. 16–17.

Antipin, V.M. 1947. Ekologiya, proiskhozhdenie i rasselenie dikikh baranov (*Ovis ammon*) Kazakhstana [Ecology, origin, and distribution of wild sheep (*Ovis ammon*) of Kazakhstan]. *Izv. AN Kazakhsk. SSR,* no. 36, *Ser. Zool.,* no. 6.

Antipin, V.M. 1955. K ekologii dzheirana i saigi (Ecology of goitered gazelle and saiga). *Priroda,* No. 7.

Antonius, O. 1912. Was ist der "Tarpan"?. *Naturwiss. Wochenschrift,* Neue Folge, vol. 11, no. 33. Berlin.

Antonius, O. 1938. On the geographic distribution in former times and today of Recent Equidae. *Proc. Zool. Soc. London,* vol. 107, pt. 4.

Anuchin, D.N. 1896. K voprosu o dikikh loshadyakh i ob ikh priruchenii v Rossii (po povodu stat'i F.P. Keppena "K istorii tarpana v Rossii") [Wild horses and their taming in Russia (with reference to F.Th. Köppen's article "On the history of tarpan in Russia")]. *Min-va Narodn. Pros., Sed'moe Desyatiletie,* pt. 305, June; pt. 306, July.

Appasov, R.N. 1958. Balantidii cheloveka, dikikh i domashnikh zhivotnykh v Kazakhstane (Balantids of man and wild and domestic animals of Kazakhstan). *Tr. In-ta Zoologii AN Kazakhsk. SSR,* no. 9.

Arens, L.E. 1957. O vliyanii zapovednosti na okhotnich'e-promyslovuyu faunu Teberdinskogo zapovednika i prilegayushchikh raionov (Effect of preserve conditions on game fauna of Teberdin preserve and adjoining regions). *Tr. Teberdinsk. Gos. Zapovadn.,* vol. 1. Stavropol.

Argentov, O.A. 1860. Oleni za-Lenskogo kraya (Deer of Trans-Lena region). *Akklimatizatsiya,* vol. 1, no. 1.

Arsen'ev, V. 1925. Gizhiginskii promyslovyi raion (Gizhiga game region). *Ekonom. Zhizn' Dal'n. Vostoka,* no. 6.

Arsen'ev, V.A. 1949. Akklimatizatsiya pyatnistogo olenya v evropeiskikh zapovednikakh SSSR (Acclimatization of sika in European preserves of USSR). *Okhrana Prirody,* no. 7.

Aspisov, D.I. 1930. Los' (*Alces alces* L.) v Tatarskoi respublike (Elk in Tatar Republic). *Mater. po Izuchen. i Okhrane Prirody TSSR,* no. 1.

Aspisov, D.I. 1956. Razmeshchenie chislennost' losei v Tatarskoi ASSR (Distribution and population dynamics of elk in Tatar Autonomous Soviet Socialist Republic). *Uch. Zap. Kazansk. Gos. Un-ta,* vol. 115, no. 8.

Astanin, L.P. 1949. Materialy po izucheniyu vozrastnoi izmenchivosti rogov krymskogo olenya (Results of study of age-related horn variations in Crimean deer). *Zool. Zhurn.,* vol. 28, no. 5.

Aul', Yu.M., Kh.I. Ling and K.L. Paaver. 1957. Mlekopitayushchie Estonskoi SSR (Mammals of Estonian Soviet Socialist Republic). Published by AN Estonsk. SSR. Tallin.

Averin, Yu.V. 1948. Nazemnye pozvonochnye vostochnoi Kamchatki (Land vertebrates of east Kamchatka). *Tr. Kronostsk. Gos. Zapovedn.*, no. 1.

Averin, Yu.V. 1949. Ekologiya kozuli (*Capreolus pygargus pygargus* Pall.) v Il'menskom zapovednike [Ecology of roe (*Capreolus pygargus pygargus* Pall.) in Il'men preserve]. *Tr. Il'mensk. Gos. Zapovedn.*, no. 4.

Averin, Yu.V. 1951. O snezhnom barane na Kamchatke (Snow sheep in Kamchatka). *Byull. Mosk. Ob-va Ispyt. Prirody, Otd. Biol.*, vol. 56, no. 1.

Averin, Yu.V. and S.L. Ushakov. 1947. Opyt akklimatzatsii pyatnistogo olenya v Il'menskom zapovednike (Work on sika acclimatization in Il'men preserve). *Tr. Il'mensk. Gos. Zapoved.*, no. 3, pt. 1.

Babenyshev, V.P. 1948. Saiga v stepyakh vostochnogo Predkavkaz'ya (Saiga in the steppes of eastern Cis-Caucasus). *Priroda,* no. 6.

Badanin, N.V. 1930. K poznaniyu gel'mintofauny dikogo kabana Pribalkhashskogo raiona (Study of helminth fauna of wild boar in Pri-Balkhash region). *Meditsinskaya Mysel' Uzbekistana i Turkmenistana,* no. 9. Tashkent.

Baikov, N.A. 1915. V gorakh i lesakh Manchzhuri (In the Mountains and Forests of Manchuria). Petrograd.

Bakeev, N.N. and A.N. Formozov. 1955. Rasprostranenie i nekotorye cherty ekologii saigi v zapadnoi chasti Pri-kaspiiskoi nizmennosti (Distribution and some characteristics of the ecology of saiga in the western part of Pri-Caspian lowland). In *Sb. Mater. po Biogeografii SSSR,* no. 2, *Tr. In-ta Geograf. AN SSSR,* vol. 66.

Bakhrushin, S.V. 1935. Ostyatskie i vogul'skie knyazhestva v XVI–XVII vv. (Ostyats and Vogul'sk principalities in the sixteenth and seventeenth centuries). *Izv. N.-I. Assots. In-ta Narodov Severa TsIK SSSR,* no. 3.

Ballantyne, E.E. 1958. Rabies control in Alberta wild-life. *Veterin. Medicine,* vol. 53, no. 2. Chicago.

Balovnev, P. 1937. Dzheiran (Goitered gazelle). *Gaz. Turkmens. Iskra,* Ashkhabad, April 11.

Banfield, A.W.F. 1954. The role of ice in the distribution of mammals. *J. Mammal.*, vol. 35, no. 1. Lawrence.

Banfield, A.W.F. 1957. The plight of barren-ground caribou. *Oryx,* vol. 4, no. 1. London.

Bannikov, A.G. 1948. Geograficheskoe rasprostranenie i zametki po biologii kulana v Mongolii (Geographic distribution and notes on the biology of kulan in Mongolia). *Zool. Zhurn.*, vol. 27, no. 1.

Bannikov, A.G. 1954. Mlekopitayushchie Mongol'skoi Narodnoi Respubliki (Mammals of Mongolian People's Republic). *Tr. Mongol'sk. Komissii AN SSSR*, no. 53.

Bannikov, A.G. 1955. O biologicheskikh gruppakh kopytnykh (Biological groups in ungulates). *Uch. Zap. Mosk. Gos. Ped. In-ta, im. V.P. Potemkina*, vol. 38, *Zoologiya*, no. 3.

Bannikov, A.G. 1958. Distribution geographique actuelle et biologie de la Saiga en Europe. *Mammalia*, vol. 22, no. 2.

Bannikov, A.G. 1958. Saigaki i biologicheskie osnovy ikh promysla (Saigas and biological foundation of their trade). *Okhota i Okhot. Khoz.*, no. 12.

Bannikov, A.G. and A.A. Fandeev. 1956. O lesokhozyaistvennom znachenii losya v Podmoskov'e (Importance of elk to forestry around Moscow). *Uch. Zap. Mosk. Gos. Ped. In-ta im. V.P. Potemkina*, vol. 61, *Zoologiya*, nos. 4–5.

Bannikov, A.G. and L.S. Lebedeva. 1956. O znachenii olenya v lesakh Belovezhskoi Pushchi (Importance of deer in Belovezh Forest woods). *Byull. Mosk. Ob-va Ispyt. Prirody, Otd. Biol.*, vol. 61, no. 4.

Barabash-Nikiforov, I.I. 1956. Novye dannye ob intensivnom rasselenii nekotorykh vidov zverei na protyazhenii poslednego desyatiletiya (New data on intense raising of some species of animals in the last decade). *Zool. Zhurn.*, vol. 35, no. 4.

Barabash-Nikiforov, I.I. 1957. Zveri yugo-vostochnoi chasti chernozemnogo tsentra (Animals in southeastern part of Chernozem Center). Voronezh.

Bashkirov, I. 1939. Kavkazskii zubr (Caucasian wisent). In Sb. *Kavkazsk. Zubr.* Moscow.

Bashkirov, I. 1939. Pervyi god raboty po vosstanovleniyu zubra i ego akklimatizatsii v Krymskom gos. zapovednike (The first year of work on restoration of wisent and its acclimatization in Crimean state preserve). In Sb. *Kavkazsk. Zubr.*, Moscow.

Bashkirov, I. and I.D. Grigor'ev. 1931. Ocherk okhotnich'ego promysla Tatarii (Outlines of game husbandry in Tatary). *Raboty Volzhsko-Kamskoi Kraevoi Prom. Biol. Stants.*, no. 1.

Bauplan. 1660. *Description de l'Ukrainie* etc. Rouen.

Bazhanov, V.S. 1929. O kochevkakh saigi (Saiga migrations). *Okhotnik*, no. 11.

Bazhanov, V.S. 1945. Materialy po ekologii i zoogeografii kopytnykh (Data on the ecology and zoogeography of ungulates). *Izu. AN Kazakhsk. SSR, Ser. Zool.*, no. 5.

Bazhanov, V.S. 1946. Zametki o nekotorykh mlekopitayushchikh basseina r. Penzhiny (Notes on some mammals in Penzhina River basin). *Byull. Mosk. Ob-va Ispyt. Prirody, Otd. Biol.,* vol. 51, nos. 4–5.

Bazhanov, V.S. 1951. Novye dannye o teriofaune vostochnogo Ust'yurta (New data on the theriofauna of east Ustyurt). *Izv. AN Kazakhsk. SSR, Ser. Zool.* no. 10.

Belevy puteshestviya cherez Rossiyu v raznye asnyatskie zemli, a imenno: v Ispagen, v Pekin, v Darbent, v Konstantinopol' (Belev's Travels through Russian to Various Parts of Asia: Ispahan, Peking, Derbent, and Constantinople). 1776. Parts 1 to 3 translated from French by M. Popov. St. Petersburg.

Belopol'skii, L.O. 1933. Parnokopytnye Anadyrsko-Chukotskogo Kraya (Artiodactyls of Anadyr-Chukchi region). *Tr. In-ta AN SSSR,* vol. 1, nos. 3–4.

Beloslyudov, B.A. 1948. Mlekopitayushchie pustyni Betpak-Dala (Mammals of Betpak-Dala desert). *Izv. AN Kazakhsk. SSR, Ser. Zool.,* no. 8.

Belousov, V.I. 1915 Opyt obsledovaniya sobolinogo promysla i promyslovoi okhoty voobshche v Cherdynskom i Verkhoturskom uezdakh Permsk. gub (Experiments in sable hunting and general game husbandry in Cherdy and Verkhotur districts of Perm state). *Mater. k. Poznan. Russk. Okhot. Dela,* no. 7, Petrograd.

Belousov, V.I. 1928. Khar. *Okhotnik i pushnik Sibiri,* no. 12.

Belousov, V.I. 1929. Perekochevka zverei (Animal migrations). *Okhotnik i Rybak Sibiri,* no. 1.

Belousov, V.I. 1934. Medvedi, berkuty i volki v zapadnykh Sayanakh (Bear, golden eagle, and wolf in western Sayans). *Okhotnik Sibiri,* nos. 5–6.

Belyaev, I.D. 1865. Pominki po vymershem ture (Requiem for dead tur). *Zap. Russk. Ob-va Akklimatiz.* Izd. Mosk. Zool. Sada.

Belyaeva, M.Ya. 1958. Gel'mintofauna mlekopitayushchikh Belovezhskoi Pushchi i nablyudeniya po epizootologii nekotorykh gel'mintozov (Helminths of mammals of Belovezh Forest and observations on epizooty of some helminthiases). Kand. Diss.

Belyk, V.I. 1948. Promyslovye zveri Yakutii (Game animals of Yakutia). In Sb. *Dokl. na Pervoi Nauchn. Sessii Yakutsk. bazy AN SSSR.* Yakutia.

Belyk, V.I. 1953. Sostav i raspredelenie okhotnich'e-promyslovoi fauny mlekopitayushchikh Yakutii (Composition and distribution of mammalian game fauna in Yakutia). In Sb. *Promysl. Fauna i Okhotn. Khoz.* Yakutii, no. 1. Yakutia.

Beme, R.L. 1957. Kraniologicheskaya kharakteristika krymskogo olenya (sravnitel'no s kavkazskim) (Craniological characteristics of Crimean deer compared with Caucasian deer). *Zool. Zhurn.*, vol. 36, no. 10.

Benson, D.A. 1957. Moose "sickness" in Nova Scotia. 1. *Canad. Journ. of Comparat. Medic. and Veterin. Soc.*, vol. 22, no. 7. Cardenvale.

Berezyuk, I.E. 1931. Dzheirany v Syugatinskoi doline (Goitered gazelle in Syugata valley). *Okhotnik,* no. 4.

Berg, L.S. and M.M. Ivanova-Berg. 1951. Tigry v Srednei Azii (Tigers in Central Asia). *Priroda,* no. 6.

Berkov, A. 1927. O saigakakh v Kalmytskoi avtonomnoi oblasti (Saiga in Kalmyk Autonomous Republic). *Okhotnik,* no. 9

Beskorovnyi, L.A. 1948. Zabolevanie sibirskogo kozeroga zlokachestvennoi goryachkoi krupnogo rogatogo skota v Almaatinskom zooparke (Infectious cattle fever in Siberian ibex in Alma-Ata Zoological Park). *Tr. Almaatinsk. Zooparka,* no. 1.

Bil'kevich, S. 1918. Kollektsiya Zakaspiiskogo Muzeya. Mlekopitayush-chie (Collection of Trans-Caspian Museum. Mammals). *Izv. Zakaspiisk. Muzeya,* vol. 1.

Bil'kevich, S. 1924. Leopardi i okhota na nego v Zakaspiiskom krae (Leopard and its hunting in Trans-Caspian region). *Turkestansk. Okhotnik,* nos. 5–8.

Birulya, A.A. 1907. Ocherki iz zhizni ptits polyarnogo poberezh'ya Sibiri (Some features of bird life on the polar coasts of Siberia). *Zap. Ak. Nauk po Fiz.-Mat. Otd.*, vol. 18, no. 2.

Bischoff. 1854. *Entwicklungsgeschichte des Rehes.* Giessen.

Blagoveshchenskii, S. 1912. Okhotnichii promysel v Olonetskoi gubernii. Pamyatnaya knizhka Olonetskoi gubernii na 1912 g. (Game hunting in Olonets Province. Gazetteer of Olonets Province for 1912). Petrozavodsk.

Bobrinskii, N.A. 1933. Geograficheskoe rasprostranenie olenei Srednei Azii (Geographic distribution of deer in middle Asia). *Zool. Zhurn.*, vol. 12, no. 4.

Bobrinskii, N.A. 1944. Otryad neparnokopytnykh (Perissodactyls). In the book *Opredelitel' Mlekopitayushchikh SSSR* by N.A. Bobrinskii, B.A. Kuznetsov and A.P. Kuzyakin. Moscow.

Bobrinskii, N.A. 1944. Otryad parnokopytnykh (Artiodactyls). In the book *Opredelitel' Mlekopitayushchikh SSSR* by N.A. Bobrinskii, B.A. Kuznetsov and A.P. Kuzyakin. Moscow.

Boev, S.N. 1957. Legochnye nematody kopytnykh zhivotnykh Kazakhstana (Pulmonary Nematodes in Kazakhstan Hoofed Animals). Alma-Ata.

Boev, S.N. and I.B. Sokolova. 1949. K poznaniyu gel'mintofauny gornogo kozla (*Capra sibirica*) Kazakhstana [Study of helminth fauna of Siberian ibex (*Capra sibirica*) in Kazakhstan]. *Izv. AN Kazakhsk. SSR,* no. 74, *Ser. Parazitol.,* p. 7.

Boev, S.N., I.B. Sokolova and V.I. Bondareva. 1948. K poznaniyu gel'mintofauny arkhara Kazakhstana (Study of helminth fauna of argali sheep in Kazakhstan). *Izu. AN Kazakhsk. SSR,* no. 44, *Ser. Parazitol.,* p. 6.

Boev, S.N., L.I. Lavrov, Ya.N. Zakhryalov and A.P. Maksimova. 1957. Materialy po gel'mintofaune dikikh zhvachnykh zhivotnykh Zapadnogo Tyan'-Shanya (Data on helminth fauna of wild ruminants of west Tien Shan). *Tr. In-ta Zoologii AN Kazakhsk. SSR,* vol. 7.

Bogdanov, M.N. 1871. Ptitsy i zveri Chernozemnoi polosy Povolzh'ya i doliny srednei i nizhnei Volgi (Birds and animals of chernozem region along the Volga and valleys of central and lower Volga). *Tr. Ob-va Estestvoisp. Pri-Kazansk. Un-ta,* vol. 1, sect. 1.

Bogdanov, M.N. 1873. Etyudy russkoi okhoty (Study of Russian game hunting). *Zhurn. Okhoty i Konnozavodstva,* nos. 1–14.

Bogdanov, M.N. 1882. Ocherki prirody Khivinskogo oazisa i pustnyi Kyzylkum (Natural Features of Khiva Oasis and Kyzylkum Desert). Tashkent.

Bogdanov, O.P. 1953. Vintorogii kozel v Baba-Tage (Markhor in Baba-Tag). *Priroda,* no. 7.

Borodin, L.P. 1940. Uchet, razmeshchenie i kormovaya baza losya v Okskom zapovednike (Census, distribution, and fodder base of elk in Oka preserve). *Tr. Oksk. Gos. Zapovedn.,* vol. 1.

Bouvier, G., H. Bourgisser and P. Schneider. 1957. Observations sur les maladies du gibier, des oiseaux et des poissons faites en 1955 et 1956. *Schweiz. Arch. Tierheilkunde,* vol. 99, no. 8.

Brandt, F. 1867. Zoogeographische und paläontologische Beiträge. *Verhandl. d. Kais. Mineralog. Ges. zu St. Petersburg, Zweite Serie.*

Brauner, A.A. 1900. Zametki o krymskom olene (Notes on Crimean deer). *Zap. Novorossk. Ob-va Estestvoisp.,* vol. 23, no. 2. Odessa.

Brauner, A.A. 1915. K kakomu vidu prinadlezhat kosuli Yuzhnoi Rossii i Kryma? (To what species do roe deer of southern Russia and Crimea belong?). *Zap. Krymsk. Ob-va Estestvoisp.,* vol. 5. Simferopol'.

Brauner, A.A. 1923. Sel'skokhozyaistvennaya zoologiya (Agricultural Zoology). Moscow.

Brinken de. 1824. *Memoire descriptif sur la foret Imperiale de Bailowieza en Lithuanie.* Varsovie.

Bromlei, G.F. 1951. Sudzukhinskii zapovednik (Sudzukhin sanctuary). In Sb. *Zapovedniki SSSR,* vol. 2, Moscow.

Bromlei, G.F. 1953. Znachenie kharzy kak khishchnika i sposoby ee unichtozheniy v Primorskom krae (Importance of yellow-throated marten as a predator and methods for liquidating it in Primor'e region). In Sb. *Preobrazovanie Fauny Pozvonochnykh Nashei Strany* (*Biotekhnicheskie Meropriyatiya*). Moscow.

Bromlei, G.F. 1956. Ekologiya dikogo pyatnistogo olenya v Primorskom krae (Ecology of wild sika in Primor'e region). In Sb. *Mater. po Rezul'tatam Izuch. Mlekopitayushchikh v Gos. Zapovedn.* Moscow.

Bromlei, G.F. 1956. Goral (*Nemorhaedus caudatus raddeanus* Heude, 1894), *Zool. Zhurn.,* vol. 35, no. 9.

Bromlei, G.F. 1956. Materialy po ekologii sobolya i kharzy, rasprostranennykh v Primorskom krae (Data on the ecology of sable and yellow-throated marten in Primor'e region). In Sb. *Mater. po Rezul'tatam Izuch. Mlekopitayushchikh v Gos. Zapovedn.* Moscow.

Broniovii de Biesdzfedea, M. 1630. Ad Tataricum legati. Tataria. "Russia seu Moscovia itemque Tataria". Ex officina Elzeviriana.

Bronnikov. 1898. Pamiry. Bolezni zhvachnykh zhivotnykh (Pamir. Diseases of ruminants). *Gaz. Turkestansk. Vedomosti,* no. 94. Tashkent.

Buechner, H.K. 1956. The future of bighorn sheep. *Animal Kingdom,* vol. 59, no. 1. New York.

Bulavin, A. 1934. O nekotorykh kopytnykh v Koshagachenskom aimake (Some ungulates in Koshagach territorial administrative unit). *Okhotnik Sibiri,* no. 3.

Burt, W.N. 1948. *Mammals of Michigan.* Ann Arbor.

Burt, W. and F. Grossenheider. 1952. A Field Guide of Mammals. Boston.

Butarin, N.S. 1947. Mezhvidovaya gibridizatsiya dikikh i domashnikh koz, kak metod sozdaniya novykh porod (Interspecies hybridization of wild and domestic goats as a method of raising new strains). *Vestn. AN Kazakhsk. SSR,* nos. 1–2 (22–23).

Butarin, N.S., P.A. Es'kov, D.M. Miletskii and N.N. Bagrovskaya. 1955. Otdalennaya gibridizatsiya dikikh svinei s domashnimi (Distant hybridization of wild hogs with domestic hogs). Alma-Ata.

Buturlin, S.A. 1913. Nablyudeniya nad mlekopitayushchimi, sdelannye vo vremya Kolymskoi ekspeditsii 1905 g. (Observations on mammals made during the 1905 Kolyma expedition). *Dnevnik Zool. Otd. Ob-va Lyubit. Est., Antrop. i Etnogr., Nov. Ser.,* vol. 1, no. 5.

Buturlin, S.A. 1934. Losi (Elk). Moscow-Leningrad.

Cabon, K. 1958. Das Massensterben von Wildschweinen im Naturstaatpark von Bialowieza im Winter 1955/1956. *Acta Theriologica,* vol. 2, no. 4.

Cabon, K. 1958. Masova smierc dzikow w Bialowieskim Parku Narodovym w zimie 1956 roku. *Chronmy Przyr. Ojez.,* vol. 14, no. 1.

Cabrera, A. and J. Yepes. 1940. *Mammiferos Sud-Americanos.* Buenos Aires.

Caesar, H. 1956. Der Einfluss der Wilddichte auf die Gewichtsentwicklung des Rotwiides im Soonwald. *Zeitschr. f. Jagdwiss.,* vol. 2, no. 1. Hamburg.

Calinescu, R. 1930. Von einigen Säugetieren Rumäniens. *Zeitschr. f. Säugetierk.,* vol. 5. Berlin.

Calinescu, R. 1931. Verzeichniss und Bibliographie der Säugetiere Rumäniens. *Zeitschr. f. Säugetierk.,* vol. 6. Berlin.

Cantemir, D. 1872. *Descriptio Moldaviae.* Bucuresci.

Carter, T.D., J.E. Hill and G.H.H. Tate. 1946. *Mammals of the Pacific World.* New York.

Charlemagne, M. 1937. Zoogeografiya URSR (Zoogeography of Ukrainian Soviet Socialist Republic). Kiev.

Charlemagne, N.V. 1949. O prezhnem rasprostranenii i istorii onagra na Ukraine (Former dispersal and history of onager in the Ukraine). *Okhrana Prirody,* vol. 9.

Charlemagne, N.V. 1953. Oleni Sovietskoi Ukrainy (Deer of Soviet Ukraine). *Priroda,* no. 4.

Charlemagne, N.V. 1955. O losyakh Ukrainy (Ukrainian elk). *Priroda,* no. 4.

Charnolusskii, V.V. 1930. Materialy po bytu loparei (Data on the life Style of Laplanders). Leningrad.

Chasen, F.N. 1940. A checklist of Malaysian mammals. *Bull. of the Raffles Museum, Singapore States Settlement,* no. 15.

Cheikin, M.I. 1914. Geograficheskii ocherk Vostochnogo Pamira (A geographic description of eastern Pamir). *Izv. Turkestansk. Otd. Russk. Geograf. Ob-va,* vol. 10, no. 1. Tashkent.

Cherkasov, A. 1867 and 1884. Zapiski okhotnika Vostochnoi Sibiri (Notes of a Hunter in Eastern Siberia). St. Petersburg, 1st ed., 1867; 2nd ed., 1884.

Chernavin, V.V. 1916. Zametki o dikikh baranakh Zapadnogo Tyan'-Shanya (Notes on wild sheep of western Tien Shan). *Ezheg. Zool. Muzeya Akad. Nauk,* vol. 21, nos. 2–3.

Chernyavskaya, S.I. 1956. Sezonnoe razmeshchenie i kochevki dikikh kopytnykh i medvedei v raione Kavkazskogo zapovednika v svyazi s raspredeleniem urozhaya plodov fruktarnikov i orekhonosov (Seasonal disposition and migrations of wild ungulates and bear in Caucasian preserve in relation to yield of fruit- and nut-bearing trees). *Byull. Mosk. Ob-va Ispyt. Prirody, Otd. Biol.,* vol. 61, no. 4.

Chernyshev, V.I. 1958. Fauna i ekologiya mlekopitayushchikh tugaev Tadzhikstana (Fauna and ecology of mammals in Tadzhikistan tugai). *Tr. In-ta Zool. i Parazitol. AN Tadzhiksk. SSR,* vol. 85.

Chizh, A.N. and M.A. Bazhenov. 1951. Gemosporidii u losya (Hemosporidia in elks). *Priroda,* no. 1.

Choquette, L.P.E., L.K. Whitten, G. Rankin and C.M. Seal. 1957. Note on parasites found in reindeer (*Rangifer tarandus*) in Canada. *Canad. Journ. of Compar. Medic. and Veterin. Soc.,* vol. 21, no. 6. Cardenvale.

Chudi. 1873. Al'piiskii mir (The Alpine World). Translated by L. and N. Verkhovskii. St. Petersburg.

Chun-Syun, F. 1958. O sluchayakh zarazheniya trikhinnellezom cherez myaso kabana (*Sus scrofa*) v Kazakhstane [Occurrence of trichinellosis through the meat of wild boar (*Sus scrofa*) in Kazakhstan]. In Sb. *Med. Parazitol. i Parazitarn. Bolezni,* vol. 27, no. 4.

Clarck, E.D. 1810. *Travels in Various Countries of Europe, Asia, and Africa.* Part I: *Russia, Tartar, and Turkey.* Cambridge.

Coon, C.S. 1951. Cave Explorations in Iran, 1949. Mus. Monograph. Philadelphia.

Corner, A.H. and R. Connell. 1958. Brucellosis in bison, elk and moose in Elk Island National Park, Alberta, Canada. *Canad. Journ. of Compar. Medic. and Veterin. Soc.,* vol. 22, no. 1. Cardenvale.

Couturier, M.A. 1938. Le Chamois (*Rupicapra rupicapra* L.). Grenoble.

Cringan, A.T. 1958. Influence of forest fires and fire protection on wild life. *Forest Chronicle,* vol. 34, no. 1. Toronto.

Crisler, L. 1956. Observations on wolves hunting caribou. *J. Mammal.,* vol. 37, no. 3.

Dal', S.K. 1930. Materialy po sistematike i biologii krymskoi kosuli (Data on the systematics and biology of Crimean roe deer). *Zap. Krymsk. Ob-va Estestvoisp. i Lyubit. Prirody,* vol. 12, Simferopol'.

Dal', S.K. 1944. Pozvonochnye zhivotnye Saraibulagskogo khrebta (Vertebrates of Sarai-Bulag range). *Zool. Sb.* (AN Armyansk, SSR), no. 3.

Dal', S.K. 1949. Ocherk pozvonochnykh zhivotnykh Aiotsdzorskogo khrebta (An outline of vertebrates of Aiotsdzor range). *Zool. Sb.* (AN Armyansk. SSR), no. 6.

Dal', S.K. 1951. Dannye po biologii, rasprostraneniyu, chislennosti i kolichestvennomu sootnosheniyu v stadakh bezoarovykh koz na Urtsskom khrebte (Data on the biology, distribution, population dynamics, and numerical ratio of bezoar goat herds in Urts range). *Izv. AN Armyansk. SSR, Ser. Biol. i S.-Kh. Nauk,* vol. 4, no. 1.

Dal', S.K. 1954. Zhivotnyi mir Armyanskoi SSR (Fauna of Armenian Soviet Socialist Republic), vol. 1. Yerevan.

Dal', S.K. 1958. Sistematicheskii obzor zhivotnykh Kryma. Zhivotnyi mir SSSR. T. 5. Gornye oblasti Evropeiskoi chasti SSSR (Systematic Review of Animals of Crimea. Fauna of the USSR, vol. 5: Montane Region of the European part of the USSR). Moscow-Leningrad.

Dal', S.K., V.M. Gusev and S.N. Bednyi. 1958. Ob ekologii i rasmnozhenii saigi (*Saiga tatarica* L.) [Ecology and reproduction of saiga (*Saiga tatarica* L.)]. *Zool. Zhurn.,* vol. 37, no. 3.

Dalmatov, D.Ya. 1849. Istoriya zubra ili tura, vodyashchegosya v Belovezhskoi Pushche Grodnenskoi gubernii (History of aurochs or tur reared in Belovezh Forest in Grodnensk province). *Lesnoi Zhurnal,* nos. 24–28.

Dalmatov, D.Ya. 1855. Zubry kak samobytnaya poroda (Wisent as an independent species). *Lesovodstvo i Okhota,* no. 42.

Danilov, D.N. 1947. Razmeshchenie i chislennost' losya, kosuli i kabana v Moskovskoi oblasti (Distribution and population dynamics of elk, roe deer, and wild boar in Moscow district). In Sb. *Ocherki Prirody Podmoskov'ya i Moskovskoi Oblasti (Klimat, Geologiya, Geomorfologiya, Pochvy i Zhivotnyi Mir).* Moscow.

Danilov, D.N. 1949. Chislennost' i razmeshchenie losei v SSSR (Population and distribution of elk in the USSR). *Okhrana Prirody,* vol. 6.

Danilov, D.N. 1950. Chislennost' i razmeshchenie losei v Gor'kovskoi obl. (Population dynamics and distribution of elk in Gorkii district). *Zool. Zhurn.,* vol. 29, no. 5.

Danilov, D.N. 1951. Rasshirenie areals losya na yuge evropeiskoi chasti SSSR (Range expansion of elk in the southern European part of the USSR). *Okhrana Prirody,* vol. 13.

Danilov, D.N. 1958. Osnovnye kormovye rasteniya promyslovykh zverei i ptits (Basic food plants of game animals and birds). *Zool. Zhurn.,* vol. 37, no. 8.

Danilovich, A.P. 1949. O nekotorykh redkikh i interesnykh zveryakh ukrainskogo Poles'ya (Some rare and interesting animals in Ukrainian woodlands). *Okhrana Prirody,* vol. 8.

Darkshevich, Ya. 1939. Akklimatizatsiya pyatnistogo olenya v zapovednike Buzulukskii bor (Acclimatization of sika in Buzuluk pine preserve). *Nauch.-Metod. Zap. Gl. Upr. po Zapovedn.,* no. 4.

Dasman, R.F. and R.D. Taber. 1956. Behavior of Columbian black-tailed deer with reference to population ecology. *J. Mammal.,* vol. 37, no. 2.

de Lukka, J. 1625. Relation de tatares parcopites et nogaes, des circassians, mingreliens . . . (Russian translation by P. Yurchenko: *Zap. Odessk. Ob-va Ist. i Drevnostei,* vol. 11, 1879).

Dement'ev, D.P. 1938. Spisok mlekopitayushchikh (Mammalia) Kirgizskoi SSR (List of Mammals of Kirgizia Soviet Socialist Republic). Frunze.

Dement'ev, D.P.1946. O rasprostranenii marala (*Cervus canadensis songaricus* Severt.) na territorii Kirgizskoi SSR [Distribution of Siberian maral (*Cervus canadensis songaricus* Severt.) in Kirgizia Soviet Socialist Republic]. *Tr. Kirgizsk. Gos. Ped. In-ta im. M.V. Frunze,* vol. 1, no. 1. Frunze.

Dement'ev, G.P. 1935. Dzeren, dzheiran, saiga (Mongolian Gazelle, Goitered Gazelle, and Saiga). Moscow.

Dement'ev, G.P. and S.S. Turov. 1951. Materialy po faune nazemnykh pozvonochnykh yugo-zapadnoi Turkmenii (Data on land vertebrates of southwest Turkmenia). In Sb. *Trudy Zool. Muzeya Pri MGU,* vol. 7.

Dement'ev, G.P., N.N. Kartashov and A.O. Tashliev. 1956. Materialy po faune nazemnykh pozvonochnykh severo-vostochnoi Turkmenii (Data on land vertebrates of northeast Turkmenia). *Tr. In-ta Biol. AN Turkmensk. SSR,* vol. 4. Ashkhabad.

Dement'ev, G.P., P.T. Tsygarev and A.I. Yanushevich. 1956. Promyslovye zveri i ptitsy Kirgizii (Game Animals and Birds of Kirgizia). Frunze.

Dement'ev, N.I. 1936. Redkii zakhod losya v tundru (Rare find of elk in the tundra). *Khozyaistvo Severa,* no. 6. Arkhangel'sk.

Demidoff, E. 1900. *After Wild Sheep in Altai and Mongolia.* London.

Demidov, G.I. 1940. O rashirenii areala kosuli na Urale (Range expansion of roe deer in the Urals). *Sovetsk. Okhotnik,* no. 6.

Demin, V.S. 1947. O svelto-serykh kozlakh v Almaatinskom zapovednike (Light gray-colored goats in Alma-Ata preserve). *Tr.*

Almaatinskogo Gos. Zapovedn., no. 4.

Demiri, M. and I. Mitru. 1956. Fauna i flora Albanii (Fauna and flora of Albania). *Priroda,* no. 8.

Denisov, V.F. 1935. Nekotorye dannye po izmenchivosti tauteke i myasnoi produktvnosti arkharov (Data on the variability of tautheca and meat productivity of argali sheep). Sb. *Vidovaya Gibridizatsiya Domashnikh Zhivotnykh s Dikimi Vidami* (*Tr. Kirgizsk. Kompl. Eksped. AN SSSR 1933–1934* gg.). Moscow-Leningrad, vol. 4, p. 3.

Denniston, R.H. 1956. Ecology, behavior, and population dynamics of Wyoming or Rocky Mountain moose (*Alces alces shirasi*). *Zoologica* (USA), vol. 41, no. 3. New York.

Derevyagin, K.M. 1930. Kosuli v Kustanaiskom okruge (Roe deer in Kustanay region). *Okhrana Prirody,* vols. 8–10.

Derevyagin, P.Ya. 1947. O sezonnykh migratsiyakh dzheirana iz Yuzhnogo Pribalkhash'ya v mezhgornuyu dolinu kalkanmataya (Seasonal migrations of goitered gazelle from southern Balkhash into Kalkan-Matai intermontane valley). *Vestn. AN kazakhsk. SSR,* no. 4, p. 25.

Derevyanko, I.L. and I.V. Zharkov. 1953. Opyt zimnei podkormki dikikh opytnykh v Kavkazskom zapovednike (Winter fattening of wild ungulates in Caucasian preserve). Sb. *Preobrazovanie Fauny Pozvonochnykh Nashei Strany* (*Biotekhnicheskie Meropriyatiya*). Moscow.

Dinesman, L.G. 1957. Materialy k lesokhozyaistvennomu znacheniyu losya v Evropeiskoi chasti SSSR (Importance of elk to forestry in the European part of the USSR). *Byull. Mosk. Ob-va Ispyt. Prirody, Otd. Biol.,* vol. 62, no. 4.

Dinesman, L.G. 1957. Vrednaya deyatel'nost' mlekopitayushchikh i ptits i zashchita ot nikh drevesno-kustarnikovykh nasazhdenii (Adverse activities of mammals and birds and protection of wooded shrub plantations from them). *Soobshchen. In-ta Lesa AN SSSR,* no. 8.

Dinnik, N.Ya. 1884. Gory i ushchel'ya Kubanskoi oblasti (Mountains and ravines of Kuban district). *Zap. Kavkazsk. Otd. Russk. Geogr. Ob-va,* vol. 13, no. 1. Tiflis.

Dinnik, N.Ya. 1884. Osetiya i verkhov'ya Riona (Ossetia and the upper reaches of Riona). *Zap. Kavkazsk. Otd. Russk. Geogr. Ob-va,* vol. 13, no. 1. Tiflis.

Dinnik, N.Ya. 1890. Puteshestvie po Digorii (Travels in Digoria). *Zap. Kavkazsk. Otd. Russk. Geogr. Ob-va,* vol. 14, no. 1. Tiflis.

Dinnik, N.Ya. 1897. Kubanskaya oblast' v verkhov'yakh r. Urushtena i Beloi (Kuban district in the upper reaches of Urushtensk and

Beloe Rivers). *Zap. Kavkazsk. Otd. Russk. Geogr. Ob-va,* vol. 19, Appendix. Tiflis.

Dinnik, N.Ya. 1900. Dikii kaban i ego obraz zhizni na Kavkaz (Wild boar and its mode of life in the Caucasus). *Priroda i Okhota,* April.

Dinnik, N.Ya. 1902. Verkhov'ya Maloi Laby i Mzymty (Upper reaches of Malyi Laba and Mzymta). *Zap. Kavkazsk. Otd. Russk. Geogr. Ob-va,* vol. 22, no. 5. Tiflis.

Dinnik, N.Ya. 1909. Istreblenie dichi v gorakh Kubanskoi oblasti (Destruction of game in Kuban district mountains). *Priroda i Okhota,* October-November.

Dinnik, N.Ya. 1912. Puteshestviya po Zakatal'skom okrugu i Dagestan (Travels through Zakatal'sk region and Dagestan). *Izv. Kavkazsk. Otd. Russk. Geogr. Ob-va,* vol. 21, no. 2, Tiflis.

Dinnik, N.Ya. 1910 and 1914. Zveri Kavkaza (Caucasian Animals). Tiflis, pt. 1, 1910; pt. 2, 1914.

Ditmar, K. 1901. Poezdka i prebyvanie v Kamchatke v 1851–1855 gg. Ch. 1. Istoricheskii otchet po putevym dnevnikam (Travels and Residence in Kamchatka from 1851 to 1855. Part 1. Historical Account Based on Travel Diaries). St. Petersburg.

Dmitriev, V.V. 1938. Kopytnye zveri Altaiskogo zapovednika i preilegayushchikh mest (Hoofed animals of Altai preserve and adjacent areas). *Tr. Altaiskogo Gos. Zapovedn.,* no. 1.

Dobrzhanskii, F.S. 1928. Ocherk maralovodstva na Yuzhnom Altai (An outline of maral raising in southern Altai). Sb. *Domashnie Zhivotnye Semipalatinskoi Gubernii,* pt. 1. *Mater. Osobogo Komiteta po Issledovaniyu Soyuznykh i Avtonomnykh Respublik,* no. 18. Leningrad.

Dogel', V.A. 1934. Zametki o faune infuzorii, naselyayushchikh zheludok severnogo olenya (Notes on infusorian fauna in the stomachs of reindeer). *Tr. Arktichesk. In-ta,* vol. 24.

Dolbonosov, G. 1957. Brakon'ery Nakazany (Poachers punished). *Okhota i Okhot. Khoz.,* no. 12.

Dolgushin, L.D. 1953. Rasselenie losya na severe Urala (Elk settlement in northern Urals). *Izv. AN SSSR, Ser. Geogr.,* no. 5.

Donaurov, S.S. and V.P. Teplov. 1938. Kaban v Kavkazskom zapovednike (Wild boar in Caucasian preserve). *Tr. Kavkazsk. Zapoved.,* no. 1.

Doppel'mair, G.G. (ed.). 1926. Sobolinyi promysel na severo-vostochnom poberezh'e Baikala (Sable Industry on the Northeast Coast of Baikal). Verkhneudinsk-Leningrad.

Dorogostaiskii, V.Ch. 1918. K rasprostraneniyu i obrazu zhizni dikikh baranov i kozlov v severo-zapadnoi Mongolii (Distribution and life history of wild sheep and goats in northwest Mongolia). *Ezhegod. Zool. Muzeya., AN SSSR,* vol. 23, no. 1.

Dreschsler, H. 1958. *Zigeuner, Stiere und Flamingos.* Jena, Leipzig.

Druri, I.V. 1949. Dikii severnyi olen' Sovetskoi Arktiki i Subarktiki (Wild reindeer of Soviet Arctic and subarctic). *Tr. Arktichesk. In-ta,* vol. 200.

Dubinin, V.V. 1952. Parazitofauna kabana del'ty Volgi (Parasite fauna of wild boar in Volga delta). *Tr. Leningr. ob-va Estestvoisp.,* vol. 71, no. 4.

Dubinin, V.B. 1954. K voprosu o fauna i ekologii mlekopitayushchikh Khavstskogo raiona Tashkentskoi oblasti Uzbekskoi SSR (Mammalian fauna and ecology of mammals of Khavasts region, Tashkent district, Uzbek Soviet Socialist Republic). *Tr. In-ta Zoologii i Parazitol. AN Uzbeksk. SSR,* vol. 3.

Dubinin, V.B. 1955. Chesotqchnye kleshchi (Acariformes, Sarcoptoidea) i chesotochnye zabolevaniya dikikh mlekopitayushchikh (Itch mites and related diseases among wild mammals). *Zool. Zhurn.,* vol. 34, no. 6.

Dubinin, V.B., R.V. Grebenyuk and V.M. Steshenko. 1958. Zudnevaya chesotka tsentral'noaziatskikh gornykh kozlov-teke (*Capra sibirica* Meyer) v Kirgizii [Scabies among Central Asian Siberian ibex (*Capra sibirica* Meyer) in Kirgizia]. *Izv. AN Kirgizsk. SSR,* no. 6.

Dubrovskii, A.N. 1940. Pushnye zveri Yamal'skogo natsional'nogo okruga (Fur-bearing animals of Yamal national district). *Tr. N.-I. In-ta Polyarn. Zemledeliya, Ser. Promysl. Khozyaistvo,* no. 13.

Dul'keit, G. 1927. Promyslovye zhivotnye Tututo-Chumikanskogo raiona (Game animals of Tuturo-Chumikansk region). *Okhotnik,* no. 1.

Dul'keit, G. 1953. Znachenie rysi i rosomakhi v prirodnom komplekse altaiskoi taigi (Importance of lynx and wolverine in the natural complex of Altai taiga). Sb. *Preobrazovanie Fauny Pozvonochnykh Nashei Strany* (*Biotekhnicheskie Meropriyatiya*). Moscow.

Dul'keit, G.D. 1956. Ocherk zimnei zhizni mlekopitayushchikh severo-vostochnogo Altaya i nekotorye voprosy rekonstruktsii ikh fauny (Description of the winter life of mammals in northeast Altai and some aspects of their restoration). *Tr. Tomsk. Un-ta,* vol. 142.

Dulkeit, G.D. and V.V. Kozlov. 1958. Materialy k faune mlekopitayushchikh zapovednika "Stolby" (Data on mammalian fauna of "Stolba" preserve). *Tr. Gos. Zapovedn. "Stolby",* no. 2. Krasnoyar.

Dunaeva, T.N. 1948. Stravnitel'nyi obzor ekologii tundrovykh polevok poluostrova Yamala (Comparative review of the ecology of tundra voles of Yamal Peninsula). *Tr. In-ta Geogr. AN SSSR,* no. 41.

D'yachkov, G. 1893. Anadyrskii krai. (Rukopis' zhitelya sela Markova) [Anadyr region (Manuscript of a resident of Markov village)]. *Zap. Ob-va Izuch. Amursk. Kraya,* vol. 2. Vladivostok.

D'yakov, Yu.V. and N.V. Aleinikev. 1956. Istoriya i nekotorye rezul'taty akklimatizatsii pyatnistogo olenya v Khoperskom zapovednike (History and some results of acclimatization of sika in Khoper preserve). *Tr. Khopersk. Gos. Zapovedn.,* no. 2. Voronezh.

Dyk, V. 1956. Srnci zwer ve Vysokych Tatrach, *Ochrana Prirody,* vol. 11, no. 1. Praha.

Dyukov, N. 1930. Dzheiran (Goitered gazelle). *Okhotnik,* no. 12.

Dyunin, A. 1926. Vesennii pavodok v Astrakhanskom zapovednike (Spring floods in Astrakhan' preserve). *Okhotnik,* no. 9.

Dzhanashvili, A.G. 1943. Gibridizatsiya dagestanskogo tura (*Capra cylindricornis* Blyth.) i domashnei kozy (*C. hircus* L.) [Hybridization of Dagestan tur (*Capra cylindricornis* Blyth.) and domestic goat (*C. hircus* L.)]. *Soobshchen. AN Gruzinsk. SSR,* vol. 4, no. 8.

Egorov, A.D. and V.B. Kuvaev. 1958. O dvukh interesnykh kormovykh rasteniyakh severnogo olenya na severo-vostoke Yakutii (Two interesting food plants for reindeer in northeast Yakutia). *Izv. AN SSSR, Ser. Biol.,* no. 2.

Egorov, O.V. 1952. Ekologiya sibirskogo gornogo kozla (Ecology of Siberian ibex). Kand. Diss.

Egorov, O.V. 1953. Materialy po razmnozheniyu i rostu sibirskogo gornogo kozla (Data on reproduction and growth of Siberian ibex). *Byull. Mosk. Ob-va Ispyt. Prirody, Otd. Biol.,* vol. 58, no. 3.

Egorova, O.V. 1955. Ekologiya sibiriskogo gornogo kozla (*Capra sibirica* Meyer) [Ecology of Siberian ibex (*Capra sibirica* Meyer)]. *Tr. Zool. In-ta AN SSSR,* vol. 17.

Ekkert, N.I. and V.V. Fedders. 1912. Pasterelloz Bolingera u dikikh i domashnikh zhivotnykh v raione Belovezhskoi Pushchi (Bolinger's pasteurellosis among wild and domestic animals in Belovezh Forest region). Sb. *Rabot v Pamyat' K.M. Sadovskogo i Vospomineniya o Nem.* St. Petersburg.

Ekvtimishvili, Z.S. 1952. Sluchai zabolevaniya tura Severtsova tsenurom (*Coenurus cerebralis*) v Gruzii [A case of infection of Severtsov's tur by coenurus (*Coenurus cerebralis*) in Georgia]. *Soobshchen. AN Gruzinsk. SSR,* vol. 13, no. 9.

Ekvtimishvili, Z.S. 1952. Vertikal'noe rasprostranenie nekotorykh kopytnykh na yuzhnom sklone Kavkazskogo khrebta (Vertical distribution of some ungulates on the southern slope of the Caucasian range). *Soobshchen. AN Gruzinsk. SSR,* vol. 13, no. 8.

Ekvtimishvili, Z.S. 1953. Materialy k izucheniyu pitaniya dagestanskogo tura (*Capra cylindricornis* Blyth.) [Data on feeding of Dagestan tur (*Capra cylindricornis* Blyth.)]. *Tr. In-ta Zool. AN Gruzinsk. SSR,* vol. 11.

Ekvtimishvili, Z.S. 1953. Stadnost' turov i sern na territorii Tberdinskogo zapovednika (Herding of tur and chamois in Teberdin preserve). *Soobshchen. AN Gruzinsk. SSR,* vol. 14, no. 5.

Ellerman, J.R., R.W. Hayman and C.W.C. Holt. 1940 and 1941. *Families and Genera of Living Rodents.* London, vol. 1, 1940; vol. 2, 1941.

Ellerman, J.R. and T.C.S. Morrison-Scott. 1951. *Checklist of Palaerctic and Indian Mammals, 1758 to 1946.* London.

Ellerman, J.R., T.C.S. Morrison-Scott and R.W. Hayman. 1953. *South African Mammals. Brit. Mus. (Nat. Hist.).* London.

Emel'yanov, A.A. 1927. Promyslovye zveri zemli orochei po dannym ekspeditsii 1924 g. (Game animals around Orochei based on data of 1924 expedition). Sb. *Proizvodit. Sil. Dal'n. Vostoka. Zhivotnyi Mir. Khabarovsk-Vladivostok,* no. 4.

Endrzheevskii, A. 1905. Ocherk zverovykh okhot v Digorii (An outline of game hunting in Digoria). *Zhurn. Psovaya i Ruzheinaya Okhota, Ezhemes. Knizhn. Prilozh. k Zhurn.,* vols. 2–3.

Enukidze, G.P. 1953. K faune mlekopitayushchikh Lagodekhskogo gos. zapovednika (Mammalian fauna of Lagodekh state preserve). *Tr. in-ta Zool. AN Gruzinsk. SSR,* vol. 12.

Erxleben, J. and P. Chr. 1777. *Systema regni animals. . . .* Lipsiae.

Eversmann, E.A. 1840 and 1850. Estestvennaya istoriya Orenburgskogo kraya (Natural History of Orenburg Region). Orenburg, 1840, pt. 1; Kazan, 1850, pt. 2.

Evert, V.K. 1947. Massovoe poyavlenie dzheirana v nizov'yakh reki Ili zimoi 1945–46 gg. (Mass appearance of goitered gazelle in the lower reaches of Ili River in the winter of 1945 to 1946). *Izv. AN Kazakhsk. SSR, Ser. Zool.,* no. 6.

Fadeev, A. 1956. Uchet saigakov (Saiga census). *Okhota i Okhot. Khoz.,* no. 4.

Falk, J.P. 1786. *Beiträge zur topographischen Kenntniss des Russischen Reiches.* St. Petersburg, vol. 3.

Falz-Fein, F. 1919. Über das letzte Auftertan des Wildpferdes in Südrussland. Taurisches Gouvernement. *Sitzungsber. d. Ges. Naturforsch. Freunde zu Berlin,* nos. 5–6. Berlin.

Favorskii, V.P. 1936. Promyslovaya fauna (Game fauna). Sb.

Okhotnich'e Promyslovoe Khozyaistvo Vostochnosibirskogo Kraya. Irkutsk.

Fedchenko, A.P. 1870. Otchet o khode Turkestanskoi ekspeditsii (Record of Turkestan expedition). *Izv. Ob-va Lyubit. Est. Antrop. i Etnogr.*, vol. 8, no. 1.

Fedchenko, A.P. 1950. V Kokandskom khanstve (In Kokand Khanate). In *Puteshestvie v Turkestan* by A.P. Fedchenko. Moscow-Leningrad.

Fedchenko, A.P. 1950. Otchet turkestanskoi uchenoi ekspeditsii obshchestva (c 16 Apr. 1869 g. po 15 Aprl. 1860 g.) [Record of Turkestan scientific expedition society (from April 16, 1869 through April 15, 1870)]. In *Puteshestvie v Turkestan* by A.P. Fedchenko. Moscow-Leningrad.

Fedosov, A.V. and K.N. Nikitin. 1951. Zhivotnyi mir Bryanskoi oblasti (Fauna of Bryansk district). Bryansk.

Fedyushin, A.V. 1929. Dinamika i geograficheskoe rasprostraranie okhotnich'ei fauny BSSR (Population Dynamics and Geographic Distribution of Game Fauna of Belorussian Soviet Socialist Republic). Minsk.

Fetisov, A.S. 1947. Sezonnye korma sibirskoi kozuli v Irkutskoi oblasti (Seasonal Food of Siberian Ibex in Irkutsk Region). Irkutsk.

Fetisov, A.S. 1953. Kozulya v Vostochnoi Sibiri (Roe Deer in Eastern Siberia). Irkutsk.

Fetisov, A.S. 1955. O rasprostranenii i zashchitno-kormovykh statsiyakh sayanskogo reliktovogo severnogo olenya (*Rangifer tarandus valentinae* Fler.) v Selenginskoi Daurii [Distribution and protected grazing habitations of relict Sayan reindeer (*Rangifer tarandus valentinae* Fler.) In Selenga, Dauriya]. *Dokl. AN SSSR*, vol. 104, no. 4.

Fetisov, A.S. 1956. Sistematicheskoe polozhenie dikogo kabana iz Vostochnoi Sibiri i severo-zapadnoi Mongolii (Systematics of wild boar of eastern Siberia and northwestern Mongolia). *Izv. Biol.-Geogr. N-L. In-ta,* vol. 16, nos. 1–4. Irkutsk.

Fetisov, A.S. and V.N. Khrustselevskii. 1948. Melekopitayushchie yugo-vostochnogo Zabaikal'ya (Mammals of southeast Trans-Baikal). *Tr. Irkutskogo Un-ta., Ser. Biol.,* vol. 3, no. 3. Irkutsk.

Filatov, D. 1910. Letnyaya i zimnyaya poezdka v s.,-z. Kavkaz v 1909 g. dlya oznakomleniya s kavkazskim zubrom (Summer and winter expeditions in northwest Caucasus in 1909 to become acquainted with Caucasian wisent). *Ezheg. Zool. Muzeya Ak. Nauk,* vol. 15, no. 4.

Filatov, D. 1912. O kavkazskom zubre (Caucasian bison). *Zap. Ak. Nauk po Fiz.-Mat. Otd.,* ser. 7, vol. 30, no. 8.

Finsh, S. 1882. Puteshestvie v Zapadnuyu Sibir' v 1876 g. (Journey into Western Siberia in 1876). Moscow.

Flerov, C. 1928. Preliminary note on the diagnostic characters of genus *Moschus* Linne (Mammalia, Cervidae). *Dokl. AN SSSR, Ser. A.*, vol. 24. Leningrad.

Flerov, C. 1930. On the classification and geographical distribution of genus *Moschus* (Mammalia, Cervidae). *Ezhegod. Zool. Muzeya AN SSSR,* vol. 31. Leningrad.

Flerov, C. 1931. A review of the elks or moose (*Alces* Gray) of the Old World. *Dokl. AN SSSR.*

Flerov, K.K. 1932. Obzor diagnosticheskikh priznakov belovezhskogo i kavkazskogo zubrov (A review of diagnostic features of Belovesh and Caucasian wisent). *Izv. AN SSSR, Otd. Mat. i Est. Nauk,* ser. 7, no. 10.

Flerov, K.K. 1932. Mlekopitayushchie Murgabskoi doliny (Mammals of Murgab valley). Sb. *Murgabsk. Parazitol. Eksped.1930 g.* (*Tr. SOPS, Ser. Turkmen.*, no. 2).

Flerov, K.K. 1933. Ocherki po mlekopitayushchim Polyarnogo Urala i Zapadnoi Sibiri (Outline of mammals of polar Ural and western Siberia). *Izv. AN SSSR, Otd. Mat. i Est. Nauk,* no. 3.

Flerov, K.K. 1934. O geograficheskom rasprostranenii i sistematike losei (Geographic distribution and taxonomy of elk). *Dokl. AN SSSR,* vol. 2, no. 2.

Flerov, K.K. 1935. Kopytnye (Ungulata) arkticheskikh stran (Ungulates of Arctic countries). In *Zveri Arktiki* by G.P. Adlerberg, et al. Leningrad.

Flerov, K.K. 1935. Kopytnye zveri Tadzhikistana (Hoofed animals of Tadzhikistan). Sb. *Zveri Tadzhikistana* (*Tr. Tadzhik. Bazy AN SSSR,* vol. 1). Moscow-Leningrad.

Flerov, K.K. 1950. Morfologiya i ekologiya oleneobraznykh v protsesse ikh evolyutsii (Morphology and ecology of deerlike animals during their evolution). Sb. *Mater. po Chetvertichnomu Periodu,* no. 2.

Flerov, K.K. 1952. Kabargi i oleni. Fauna SSSR. Mlekopitayushchie (Musk Deer and Deer. Fauna of the USSR. Mammals). Moscow-Leningrad, vol. 1, no. 2.

Flerov, K.K. and I.M. Gromov. 1935. Ekologicheskii ocherk mlekopitayushchikh Nizhnego Vakhsha (Ecological features of the mammals of Lower Vakhsh). Sb. *Mater. po Parazitol. i Faune Yuzhn. Tadzhikistana* (*Tr. Tadzhik. Kompl. Eksped. AN SSSR,* 1932, no. 1). Moscow.

Föhlisch, A. 1880. *Über den Schwarzwilds chaden in West-deutschland und Mittel zu dessen Beseitigung mit Bezonderer Berücksichtigung Badens.*

Formozov, A.N. 1935. Kolebaniya chislennosti promyslovykh zhivotnykh (Population Changes of Game Animals). Moscow-Leningrad.

Formozov, A.N. 1946. Snezhnyi pokrov kak faktor sredy, ego znachenie v zhizni mlekopitayushchikh i ptits (Snow Cover as an Environmental Factor and Its Importance in the Life of Mammals and Birds). Moscow.

Formozov, A.N. 1947. Fauna. Sb. *Priroda Goroda Moskvy i Podmoskov'ya.* Moscow-Leningrad.

Formozov, A.N. 1950. Zhivotnyi mir (Animal World). Sb. *Kazakhstan. Obshchaya Fiziko-Geograficheskaya Kharakteristika.* Moscow-Leningrad.

Formozov, A.N. 1952. Sputnik sledopyta (Pathfinder's Companion). Moscow.

Fortunatov, B.K. 1925. Gibridnye stada za poslednie gody (Hybrid herds of recent years). Sb. *Askaniya Nova Stepnoi Zapovednik Ukrainy.*

Frechkop, S. 1958. *Mammiferes. Faune de Belgigue.* Bruxelles.

Galin, A.M. 1881. Olen' i okhota za nim na Srednem Urale (Deer and its hunting in middle Asia). *Priroda i Okhota,* May.

Galuzo, I.G. 1953. Krovososushchie kleshchi Kazakhstana (Blood-Sucking Mites in Kazakhstan). Alma-Ata, vols. 1–5.

Gassovskii, G.N. 1927. Gilyui-Ol' doiskii okhotnich'e-promyslovyi raion. Rezul'taty zimnei ekspeditsii 1925–1926 gg. (Gilyuy-Ol'doisk game region. Results of 1925–1926 winter expedition). Sb. *Proizvodit. Sily. Dal'n. Vostoka. Zhivotnyi Mir,* no. 4. Khabarov-Vladivostok.

Gavrilov, V.I. 1947. Zametki po biologii snezhnogo barana v Khronotskom zapovednika (Notes on the biology of snow sheep in Kronots preserve). *Zool. Zhurn.,* vol. 26, no. 6.

Gavrin, V.F. and S.S. Donaurov. 1954. Volk v Belovezhskoi Pushche (Wolf in Belovezh Forest). *Zool. Zhurn.,* vol. 33, no. 4.

Gebler, F. 1837. Übersicht des Katunishchen Gebirges der höchsten Spitze des Russischen Altai. *Mem. Acad. Im. Sc.,* vol. 3, St. Petersburg.

Glitsch, S. 1865. Beiträge zur Naturgeschichte der Antilope Saiga. *Bull. Soc. Imp. Natur. de Moscow,* vol. 38. Moscow.

Gmelin, S. 1806. Puteshestvie po Rossi dlya issledovaniya vsekh trekh tsarstv prirody (Travels in Russia for the Study of All Three Natural Kingdoms). St. Petersburg.

Golovin, D. 1925. Bedstvennoe polozhenie okhotnich'ego khozyaistva Azerbaidzhana (Disastrous situation of game husbandry in Azerbaizhan). *Okhotnik,* no. 3.

Golovin, D.N. 1901. Ocherki okhoty na Pamirakh (An outline of hunting in the Pamir). *Priroda i Okhota,* July–August.

Golovin, Yu. 1958. Kabany v Belgorodskoi oblasti (Boar in Belgorod district). *Okhota i Okhot. Khoz.,* no. 9.

Goncharov, M. 1930. Pastbishchnyi vopros v probleme gosudarst vennogo olenevodstva na Kamchatke (Problem of pasture in state deer farms of Kamchatka). *Rybn. Khoz. Dal'n. Vostoka,* nos. 5–6, Vladivostok.

Goodwin, G.G. 1946. Mammals of Costa Rica. *Bull. Amer. Mus. Nat. Hist.,* vol. 87, art. 5.

Gorbunov, E.I. 1939. K voprosu o prodolzhitel'nosti beremennosti vazhenok severnykh olenei (On the question of prolongation of gestation in reindeer). *Tr. N.-I. In-ta Polyarn. Zemledeliya, Ser. Promysl. Khozyaistvo,* no. 5.

Graf, W. 1956. Territorialism in deer. *J. Mammal.,* vol. 37, no. 2. Lawrence.

Grave, G.L., M.A. Emel'yanov, S.A. Plyushchenkov and E.A. Shmidt. 1951. Zhivotnyi mir Smolenskoi oblasti. Pozvonochnye zhivotnye (Fauna of Smolensk Region. Vertebrates). Smolensk.

Greve, C. 1898. Die verbreitung der Saiga—Antilope einst und jetzt. *Korr.-Blatt Naturforsch,* vol. 16. Riga.

Grigoryan, G.A. 1949. Paraziticheskie chervi bezoarovykh koz Armenii (Parasitic worms of Armenian bezoar goat). *Tr. N.-I. Veterin. In-ta Min-va S.-Kh. Armyansk, SSR,* no. 6.

Grigoryan, G.A. 1949. K izucheniyu fauny paraziticheskikh chervei dikikh zhvachnykh Armenii i ikh roli v rasprostranenii gel'mintozov sredi domashnikh ovets i koz (A study of the fauna of parasitic worms of wild ruminants of Armenia and their role in the spread of helminthiasis among domestic sheep and goats). *Tr. N.-I. Veterin. In-ta Min-va S.-Kh. Armyansk. SSR,* no. 6.

Grim, A. 1937. Dzheirany yagnyatsya (Parturition in goitered gazelle). *Kommunist Tadzhikistana,* April 18. Stalinabad.

Gromov, I.M. 1937. K faune i ekologii mlekopitayushchikh severo-vostochnogo Badkhyza (Fauna and ecology of mammals of north-east Badkhiz). Sb. *Problemy parazitologii i Fauny Turkmenii (Tr. SOPS, Ser. Turkmensk.,* no. 9). Moscow-Leningrad.

Gromov, S. 1958. Losi rasshiryayut svoi areal (Elk enlarge their range). *Okhota i Okhot. Khoz.,* no. 10.

Gromov, V.I. 1948. Paleontologicheskoe i arkheologicheskoe obosnovanie stratigraffii kontinental'nykh otlozhenii chetvertichnogo perioda na territorii SSSR (mlekopitayushchie, paleolit) [Paleontological and archeological basis of stratigraphy of continental formations of the Quaternary period in the territory of the USSR (Mammals, Paleolithic)]. *Tr. Inst. Geol. Nauk,* no. 64. Moscow-Leningrad.

Gromova, V.I. 1930. Tur i drevneishaya istoriya domashnego byka v SSSR (Tur and the prehistoric records of domestic bull in the USSR). *Priroda,* nos. 7–8

Gromova, V.I. 1931. Pervobytnyi byk ili tur (*Bos primigenius* Boj.) v SSSR [Primeval bull or tur (*Bos primigenius* Boj.) in the USSR]. *Ezhegod. Zool. Muzeya AN SSSR,* vol. 32, no. 3.

Gromova, V.I. 1935. Pervobytnyi zubr v SSSR (Primeval wisent in the USSR). *Tr. Zool. In-ta AN SSSR,* vol. 2.

Gromova, V.I. 1940. Ob iskopaemykh ostatkakh kozy i drugikh domashnikh zhivotnykh v SSSR (Fossil remains of goats and other domestic animals in the USSR). *Problemy Proiskhozhdeniya, Evolyutsii i Porodoobrazovaniya Domashnikh Zhivotnykh,* no. 1.

Gromova, V.I. 1949. Istoriya loshadei (roda *Equus*) v Starom Svete [History of horses (genus *Equus*) in the Old World]. *Tr. Paleontolog. In-ta AN SSSR,* vol. 17, nos. 1–2.

Grum-Grzhimailo, G.E. 1914. Zapadnya Mongoliya i Uryankhaiskii krai (Western Mongolia and Uryankhai Region). St. Petersburg, vol. 1.

Grunin, K.Ya. 1949. Novye roda podkozhnykh ovodov aziatskikh antilop (New genera of skin gadflies in Asian antelopes). *Dokl. AN SSSR,* vol. 64, no. 4.

Grunin, K.Ya. 1950. Ovoda dzerena (*Procapra gutturosa* Gm.) iz Mongol'skoi Narodnoi Respubliki [Gadflies in gazelle (*Procapra gutturosa* Gm.) in Mongolian People's Republic]. *Dokl. AN SSSR,* vol. 73, no. 4.

Grunin, K.Ya. 1956. Podkozhnye ovoda (Diptera, Hypodermatidae) dzheirana (*Gazella subgutturosa* Gmel.) [Skin gadflies (Diptera and Hypodermatidae) in goitered gazelle (*Gazella subgutturosa* Gmel.)]. *Entomol. Obozrenie,* vol. 35, no. 3.

Grunin, K.Ya. 1957. Nosoglotochnye ovoda (Destridae) [Nasopharyngeal gadflies (Oestridae)]. *Fauna SSSR. Nasekomye Dvukrylye,* vol. 19, no. 3.

Gul'misiryan, N.G. 1944. Nekotorye nablyudeniya po saige v Erevanskom Zoologicheskom parke (Some observations on saiga in Yerevan Zoological Park). *Tr. Erevanskogo Zooparka,* nos. 1–2.

Gureev, A.A. 1937. Zametki o mlekopitayushchikh Kerkinskogo okruga (Notes on mammals of Karkinsk region). Sb. *Problemy Parazitologii i Fauny Turkmenii.* Moscow-Leningrad.

Gutira, F. and I. Marek. 1931. Chastnaya patologiya i terapiya domashnikh zhivotnykh (Special Pathology and Treatment of Domestic Animals). Moscow, vol. 1.

Hainard, R. 1949. *Les mammiferes sauvages d'Europe.* Neuchâtel, Paris, vols. 1 and 2.

Haltenorth, Th. 1958. Der widerentdeckte mesopotamische Damhirsch. *Kosmos, Jahrg.*, vol. 54, no. 7.

Harper, F. 1940. Nomenclature and type localities of certain Old World mammals. *J. Mammal.*, vol. 21, no. 2.

Harper, F. 1945. *Extinct and Vanishing Mammals of the Old World.* New York.

Heck, L. 1930. Unpaar hufer. *Brehms Tierleben,* vol. 12. Leipzig.

Heim de Balzac, H. 1936. *Biogeographie des mammiferes et des oiseaux de l'Afrique du Nord.* Paris.

Hempel, G.L., W. Noak, J. Sir and H. Zimpel. 1956. *Jagd und Wild.* Berlin.

Hennert, 1797. *Über den Raupenfrass und Windbruch in der Kgl. Preussischen Forsten, 1791–1794.* Berlin.

Heptner, V.G. 1926. Kratkii opredelitel' mlekopitayshchikh Dagestana (Brief Descriptions of Dagestan Mammals). Makhach-Kala.

Heptner, V.G. 1929. Ob olene severo-zapadnogo Taimyra (Deer of northwest Taimyr). *Okhotnik,* no. 7.

Heptner, V.G. 1930. Materialy k poznaniyu raspredeleniya i biologii belugi (*Delphinapterus leucas* Pall.) [Data on the distribution and biology of beluga (*Delphinapterus leucas* Pall.)]. *Tr. N.-I. In-ta Zoologii* (*Mosk. Un-T*), vol. 4, no. 2.

Heptner, V.G. 1934. Notiz über den südrussischen Tarpan, *Zeitschr. f. Säugetierk.* vol. 9. Berlin.

Heptner, V.G. 1936. Materialy po mlekopitayushchim ostrova Diksona, prilezhashchei chasti severo-zapadnogo Taimyra i Karskogo morya (Data on mammals of Dikson Island, adjacent part of northwest Taimyr, and Kara Sea). *Sb. Trud. Gos. Zool. Muzeya Pri MGU,* vol. 3.

Heptner, V.G. 1936. Obshchaya zoogeografiya (General Zoogeography). Moscow.

Heptner, V.G. 1939. Zoogeograficheskie osobennosti fauny pustnyi Turkestana i ee proiskhozhdenie (Zoogeographic characteristics of Turkestan desert fauna and its origin). *Byull. Mosk. Ob-va Ispyt. Prirody, Otd. Biol.,* vol. 47, nos. 5–6.

Heptner, V.G. 1940. Nekotorye redkie i interesnye khishchnye i kopytnye Moskovskogo zooparka (Some rare and interesting predators and ungulates in Moscow Zoological Park). *Tr. Mosk. Zooparka,* vol. 1.

Heptner, V.G. 1946. Pustynno-Stepnaya fauna Palearktiki i ochagi ee razvitiya (Desert-steppe fauna of the Palearctic and foci of its growth). *Byull. Mosk. Ob-va Ispyt.,* vol. 50, nos. 1–2.

Heptner, V.G. 1948. Kulan i perspektivy ego sushchesvovaniya v SSSR (Kulan and the prospects of its survival in the USSR). *Okhrana Prirody,* vol. 2.

Heptner, V.G. 1948. Primenenie samoleta dlya zoologicheskikh issledovanni (Use of airplanes for zoological studies). *Vestn. mosk. Un-ta,* no. 3.

Heptner, V.G. 1949. Novye dannye po rasprostraneniyu nekotorykh pozvonochnykh Turkmenii ikh zoogeograficheskoe znachenie (Recent data on distribution of some vertebrates of Turkmenia and their zoogeographic importance). *Vestn. Mosk. Un-ta,* no. 6.

Heptner, V.G. 1950. Dzheiran (Goitered gazelle). Sb. *Okhotnich'i Prostory.* Moscow.

Heptner, V.G. 1955. Zametki o tarpanakh (Notes on tarpan). *Zool. Zhurn.,* vol. 34, no. 6.

Heptner, V.G. 1956. Fauna pozvonochnykh zhivotnykh Badkhyza (Yuzhnyi Turkmenistan) [Vertebrate Fauna of Badkhiz (Southern Turkmenistan)]. Ashkhabad.

Heptner, V.G. 1960. Dinamika areala nekotorykh kopytnykh i antropokul'turnyi faktor (Range dynamics of some ungulates and the anthropocultural factor). Sb. *Voprosy Geografii,* no. 48. Moscow.

Heptner, V.G. and A.N. Formozov. 1941. Mlekopitayushchie Dagestan (Mammals of Dagestan). Sb. *Trud. Gos. Zool. Muzeya Pri MGU,* vol. 6.

Heptner, V.G. and V.I. Tsalkin. 1947. Oleni gruppy *elaphus* L. (Deer of group *elaphus* L.). In *Oleni SSSR* (*Sistematika i Zoogeografiya*) by V.G. Heptner and V.I. Tsalkin. Moscow.

Heptner, V.G., L.G. Turova-morozova and V.I. Tsalkin. 1950. Vrednye i poleznye zveri rainov polezashchitnykh nasazhdenii (Harmful and Useful Animals in the Zone of Field Protecting Belts). Moscow.

Herre, W. 1956. *Rentiere. Die neue Brehm-Bücherei.*

Hilzheimer, M. 1926. Säugetierkunde und Archöologie. *Zeitschr. f. Säugetierk.,* vol. 1.

Hilzheimer, M. 1928. *Dama schaeferi* Hilz. *Zeitschr. f. Saugetierk,* vol. 11.

Hilzheimer, M. 1930. Paarhufer. In *Brehm's Tierleben,* vol. 13. Leipzig.

Hollister, N. 1913. Description of a new gazelle from Mongolia. *Proc. U.S. Nat. Mus.,* no. 19.

Honess, R. and K. Winters. 1956. ". . . What about the bighorn?" *Wyoming Wildlife,* vol. 10, no. 2. Cheyenne.

Ickermann, E.K. 1956. *Das Damwild.* Hamburg-Berlin.

Igoshina, K.N. 1936. Soderzhimoe rubtsa olenya v snezhnyi period goda (Rumen content of deer in the snowy period of the year). *Sov. Olenevodstvo,* no. 6.

Igoshina, K.N. and E.F. Florovskaya. 1939. Ispol'zovanie pastbishch i vypas olenei na Pripolyarnom Urale (Use of pastures and grazing of deer in the polar Urals). *Tr. N.-I. In-ta Polyarn. Zemledeliya, Ser. Olenevodstvo,* no. 8.

Il'ina, G.I. 1956. Ekologicheskie osobennosti pyatnistogo olenya i perspektivy ego akklimatizatsii v Evropeiskoi chasti SSSR (Ecological characteristics of sika and prospects of their acclimatization in the European part of the USSR). *Uch. Zap. Mosk. Ped. In-ta im. V.P. Potemkina, Kaf. Zool.,* vol. 61, nos. 4–5.

Inyakova, A.P. 1957. K voprosu chislennosti i raspredeleniya okhotnich'e-promyslovykh zhivotnykh v Teberdinskom zapovednskom zapovednike (1953–1955) [Population and distribution of game animals in Teberdin preserve (1953 to 1955)]. *Tr. Teberdinsk. Gos. Zapovedn.,* vol. 1. Stavropol.

Inyakova, A.P. 1957. K voprosu razmnozheniya zapadnokavkazskogo tura v nevole (Reproduction of west Caucasian tur in captivity). *Tr. Teberdinsk. Gos. Zapovedn.,* vol. 1. Stavropol.

Inyakova, A.P. 1957. Opyt soderzhaniya sern *Rupicapra rupicapra caucasica* Lyd. v nevole (Raising of chamois *Rupicapra rupicapra caucasica* Lyd. in captivity). *Tr. Teberdinsk Gos. Zapovedn.,* vol. 1. Stavropol.

Iokhel'son, V.I. 1898. Ocherk zveropromyshlennosti i torgovli mekhami v Kolymskom okruge (Description of trade in animals and fur in Kolyma region). *Tr. Yakutsk. Eksped., Otd.* 3, vol. 10, pt. 3. St. Petersburg.

Isakov, Yu.A. 1939. Materialy po faune mlekopitayushchikh srednei i svernoi Karelii (Mammalian fauna of central and northern Karelia). *Byull. Mosk. Ob-va Ispyt. Prirody, Otd. Biol.,* vol. 48, nos. 2–3.

Ishunin, G.I. 1948. Dzheiran (Goitered gazelle). *Okhota i Okhot. Khoz.,* no. 8.

Ishunin, G.I. and E.P. Korovin. 1945. Zapovednik kulana onagra v Badkhyze (Kulan preserve in Badkhiz). *Priroda,* no. 4.

Ismagilov, M.I. 1954. K ekologii dzheirana na o. Barsa-Kel'mes (Ecology of goitered gazelle on Bars-Kel'mes Island). *Byull. Mosk. Ob-va Ispyt. Prirody, Otd. Biol.,* vol. 60, no. 6.

Itogi perepisi severnykh okrain Dal'ne-Vostochnogo kraya (1926–1927 g.) [Results of Census in Northern Parts of the Far East (1926–1927)]. 1929. Blagoveschansk.

Ivanauskas, T.L. 1957. Promyslovaya faune Litvy i meropriyatiya po ee obogashcheniyu (Game fauna of Lithuania and measures for enriching it). *Okhrana Prirody i Zapovednoe Delo v SSSR, Byull.,* no. 2.

Ivanenko, I. 1955. K voprosu o razvitii sredneaziatskogo dikogo kabana v post-embrional'nyi period (Growth of middle Asiatic wild boar in the postembryonic period). *Uch. Zap. Tadzhiksk. Un-ta,* vol. 6, no. 1.

Ivanenko, I.D. 1956. Postnatal'noe razvitie kabana v svyazi s usloviyami vneshnei sredy (Postnatal growth of boar in relation to external environmental factors). *Izd. Tadzhiksk. Un-ta.* Stalinabad.

Ivanov, D. 1885. Okhota na Pamire (Hunting in Pamir). *Priroda i Okhota,* January.

Ivanov, V.V. 1953. Saigaki v Prikaspiiskikh stepyakh (Saiga in Pri-Caspian steppes). *Priroda,* no. 8.

Izmailov, I.V. 1940. Fauna ptits i mlekopitayushchikh Khoperskogo gos. zapovednika (Birds and mammals of Khoper state preserve). *Tr. Khopersk. Gos. Zapovedn.,* no. 1. Voronezh.

Jacobi, A. 1931. *Das Rentier, Zoologischer Anzeiger.* vol. 96. Ergänzungsband, Leipzig.

Kadenatsii, A.N. 1958. Gel'mintofauna mlekopitayushchikh Kryma i opyt ozdorovleniya domashnikh zhivotnykh ot osnovnykh gel'mintozov (Helminth fauna of Crimean mammals and prophylaxis of domestic animals for major helminthic diseases). Kand. Diss.

Kadenatsii, A.N. 1958. K poznaniyu gel'mintofauny kabargi (*Moschus moschiferus* L.) [Study of helminth fauna of musk deer (*Moschus moschiferus* L.)]. *Tr. In-ta Zool. AN Kazakhsk. SSR,* vol. 9.

Kalela, O. 1948. Occurrence of roe deer in Finland and changes in its distribution in adjoining areas. *Suomen Riista,* no. 3.

Kaletskaya, M.L. 1953. Fauna mlekopitayushchikh Darvinskogo zapovednika i ee izmeneniya pod vliyaniem vodokhranilishcha (Mammalian fauna of Darwin preserve and its changes under the influence of a water reservoir). Sb. *Rybinskoe Vodokhranilishche,* pt. 1. Moscow.

Kaletskaya, M.L. 1957. Rol' rezhima Rybinskogo vodokhranilishcha v zhizni mlekopitayushchikh Darvinskogo zapovednika (Role of Rybinsk water reservoir system in the life of mammals of Darwin preserve). *Tr. Darvinsk. Gos. Zapovedn.,* no. 4.

Kalinovskii, A.A. 1901. Ocherk kavkazskoi fauny i kavkazskikh okhot (Outline of Caucasian Fauna and Its Hunting). Tiflis.

Kalnin'sh, A.I. 1950. Okhota i okhotnich'e khozyaistvo v Latvinskoi SSR (Hunting and Its Economy in Latvian SSR). Riga.

Kalugin, S.G. 1958. Zubry v estestvennykh usloviyakh Kavkazskogo zapovednika (Wisent in the natural environment of Caucasian preserve). *Tr. Kavkazsk. Gos. Zapovedn.,* no. 4. Maikop.

Kamenskaya, M.A. 1956. O kormakh zubra v Prioksk-Terrasnom zapovedn. (Food of wisent in Priok-Terras preserve). *Uch. Zap. Mosk. Gor. Ped. In-ta im. V.P. Potemkina,* vol. 61.

Kantemir, D. 1716. *Descriptio Moldaviae.*

Kantemir, D. 1769. Beschreibung der Moldau. *Magaz. f. d. neue Historie und Geographie angelegt von. D. Anton Friedrich Büsching.* Hamburg.

Kantemir, D. 1789. Istoricheskoe, geograficheskoe i politicheskoe opisanie Moldavii (Historical, Geographic, and Political Description of Moldavia). (Translated from German).

Kaplanov, L.G. 1935. Biologiya i promysel losya v basseine r. Dem'yanki (Biology and hunting of elk in Dem'yanka River basin). In *Los' i ego promysel* by P.B. Yurgenson et al. Moscow.

Kaplanov, L.G. 1948. Izyubr' srednego Sikhote-Alinya (Manchurian wapiti of central Sikhote-Alin). In *Tigr, Izyubr', Los'* by L.G. Kaplanov. *Mater. k Poznan. Fauny i Flory SSSR, Nov. Ser., Otd. Zool.,* no. 14, p. 29.

Kaplanov, L.G. 1948. Los' v Sikhote-Alin'skom zapovednike (Elk in Sikhote-Alin Preserve). In *Tigr, Izyubr', Los'* by L.G. Kaplanov. *Mater. k Poznan. Fauny i Flory SSSR, Nov. Ser., Otd. Zool.,* no. 14, p. 29.

Kaplanov, L.G. 1948. Tigr v Sikhote-Alin (Tiger in Sikhote-Alin). In *Tigr, izyubr', Los'* by L.G. Kaplanov. *Mater. k Poznan. Fauny i Flory SSSR, Nov. Ser., Otd. Zool.,* no. 14, p. 29.

Karacharovskii, V.V. 1951. Pozdnechetvertichnaya fauna basseina r. Yuryuzani (Yuzh. Ural) [Late Quaternary fauna of Yuryuzana River basin (southern Ural)]. *Mater. i Issledov. po Arkheol. SSSR,* vol. 21.

Karelin, G.S. 1875. Razbor stat'i A. Ryabinina "Estestvennye proizvedeniya zemel' Ural'skogo Kazach'ego Voiska" (An analysis of A. Ryabinin's article "Natural products of Ural Kazach Voisk"). *Tr. SPb. Ob-va Estestvoisp.,* vol. 6. St. Petersburg.

Kartsov, G. 1903. Belovezhskaya Pushcha. Ee istoricheskii ocherk, sovremennoe okhotnich'e khozyaistvo i t.d. (Belovezh Forest. Its History and Present Hunting Prospects). St. Petersburg.

Kashchenko, N.F. 1900. Opredelitel' mlekopitayushchikh Tomskogo kraya (Identification of mammals of Tomsk region). *Izv. Tomsk. Un-ta,* vol. 18.

Kashchenko, N.F. 1900. Rezul'taty Altaiskoi zoologicheskoi ekspeditsii 1898 g. (Results of Altai zoological expedition of 1898). *Izv. Tomsk. Un-ta,* vol. 16.

Kashchenko, N.F. 1902. Mlekopitayushchie, sobrannye Altaiskoi ekspeditsiei P.G. Ignatova v 1901 g. (Mammals collected by P.G.

Ignatov in 1901 Altai expedition). *Ezhegod. Zool. Muzeya. Akad. Nauk,* vol. 7.

Kashkarov, D.N. 1927. Rezul'taty ekspeditsii Gl. Sr.-Az. muzeya v raion oz. Sary-Chilek (Results of Major Central Asian Museum Expedition into the Region of Lake Sary-Chilek). Tashkent, pt. 1.

Kashkarov, D.N. 1934. Ekologicheskii ocherk fauny pozvonochnykh Arslanboba (Sev. Ferghana) [Ecology of vertebrate fauna of Arslanbob (northern Ferghana)]. Sb. *Voprosy Ekologii i biotsenol,* no. 1.

Kashkarov, D.N. 1937. Ekologiya domashnikh zhivotnykh, ee soderzhanie, zadachi i metody (Ecology of domestic animals, its scope, problems, and methods). Sb. *Pamyati ak. M.A. Mezbira.* Moscow-Leningrad.

Kaznevskii, P.F. 1954. Reakklimatizatsiya marala na Yuzhnom Urale (Reacclimatization of maral in southern Ural). *Priroda,* no. 2.

Kaznevskii, P.F. 1956. Rasselenie marala na Yuzhnom Urale (Colonization of maral in southern Ural). *Zool. Zhurn.,* vol. 35, no. 10.

Kaznevskii, P.F. 1958. Problema sokhraneniya chislennosti olenei v Voronezhskom zapovednike (Problems of preserving the deer population in Voronezh preserve). *Okhrana Prirody Tsentral'no-Chernozemnoi Polosy.* Voronezh, vol. 1.

Kenneth, J.H. 1943. *Gestation Periods. A Table and Bibliography.* London.

Kessler, K.F. 1851. Zhivotnye gubernii Kievskogo uchebnogo okruga (Animals of Kiev experimental district). In *Chast Sistematicheskaya. Zhivotnye Mlekopitayushchie.* Kiev.

Khakhlov, V.A. 1928. Zaisanskaya kotlovina i Tarbagatai (Zaisan Depression and Tarbagatai). Tom'sk.

Kholostov, V.G. 1956. Kaban v Arkhangel'skoi oblasti (Boar in Arkhangelsk district). *Byull. Mosk. Ob-va Ispyt. Priody, Otd. Biol.,* vol. 61, no. 4.

Kirikov, S.V. 1935. Ekologiya fauny pozvonochnykh Predural'ya i Zaural'ya na ikh yuzhnoi razgranichitel'noi linii (Ecology of vertebrate fauna of Cis-Ural and Trans-Ural at their southern boundary). *Zool. Zhurn.,* vol. 24, no. 3.

Kirikov, S.V. 1952. Ptitsy i mlekopitayushchie v usloviyakh landshaftov yuzhnoi okonechnosti Urala (Birds and Mammals under the Topographic Conditions of the Southern Extremity of Urals). Moscow.

Kirikov, S.V. 1952. Istoricheskie izmeneniya zhivotnogo mira nashei strany v XIII–XIX vv. (Historical changes in fauna of our country from the thirteenth to the nineteenth centuries). *Izv. AN SSSR, Ser. Geograf.,* no. 6.

Kirikov, S.V. 1953. Istoricheskie izmeneniya zhivotnogo mira nashei strany v XIII–XIX vv. Soobshch. 2-e (Historical changes in fauna of our country from the thirteenth to the nineteenth centuries. Report No. 2). *Izv. AN SSSR, Ser. Geograf.,* no. 4.

Kirikov, S.V. 1955. Istoricheskie izmeneniya zhivotnogo mira nashei strany v XIII–XIX vv. Soobshch. 3-e (Historical changes in fauna of our country from the thirteenth to the nineteenth centuries. Report no. 3). *Izv. AN SSSR, Ser. Geograf.,* no. 1.

Kirikov, S.V. 1955. Ptitsy i mlekopitayushchie yuzhnoi okrainy Priural'ya (Birds and mammals of southern Cis-Ural region). Sb. *Mater. po Biogeografii SSSR,* no. 2.*Tr.In-ta Geografii AN SSSR,* vol. 66.

Kirilov, N. 1902. Okhotnich'e khozyaistvo v Zabaikal'skoi obl. (Importance of game in Trans-Baikal district). *Priroda i Okhota,* January.

Kirshenblat, Ya.D. 1951. Polovye tsikly samok mlekopitayushchikh (Sex cycles in female mammals). *Priroda,* no. 10.

Kir'yakov. 1837. Khersonskie stepi (Kherson steppes). *Lesnoi Zhurnal,* no. 4.

Kissling, W. 1925. *Das Schwarzwild.* Berlin.

Klemm, M. 1951. Das Schwarzwild und die biologische Bekämpfung unserer Forstschädlinge. *Nachrichtenblatt der deutschen Pflanzenschutzdienstes,* N.F., vol. 5.

Klyushkin, E.A. 1949. Oleni v Dargan-Ata (Turkmeniya) [Deer in Dargan-Ata (Turkmenia)]. *Okhrana Prirody,* vol. 7.

Klyushkin, E.A. 1950. Okhrana prirody v Turkmenistane (Conservation of nature in Turkmenistan). *Izv. Turkmansk. Fil. AN SSSR,* no. 2.

Klyushkin, E.A. 1954. Zamtki o tugainom olene (Notes on tugai deer). *Izv. AN Turkmansk.* SSR, no. 2.

Knize, A.A. 1935. Promysel losya v Karel'skoi ASSR i Leningradskoi oblasti (Hunting for elk in Karelian Autonomous Soviet Socialist Republic and Leningrad district). In *Los' i Ego Promysel* by P.B. Yurgneson et al. Moscow.

Knorre, E.P. 1939. Itogi dvukhletnikh opytov po odomashnivaniyu losya (Results of two-year experiments on domestication of elk). *Nauch.-Metod. Zap. Gl. Upr. po Zapovedn.,* no. 4.

Knorre, E.P. 1949. Ekologiya losya v svyazi s ego odomashnivaniem (Ecology of elk in relation to its domestication). *Nauch.-Metod. Zap. Gl. Upr. po Zapovedn.,* no. 13.

Knorre, E.P. 1953. Otlov, vyrashchivanie i trenirovka losyat (primenitel'no k prirodnym usloviyam severotaezhnoi zony SSSR) dlya obsluzhivaniya okhotnich'ego promysla [Trapping, raising, and training elk young (in relation to natural conditions of northern taiga zone of the USSR) for the purpose of sustaining game hunting]. Sb. *Preobrazovanie Fauny Pozvonochnykh Nashei Strany* (*Biotekhnicheskie Meropriyatiya*). Moscow.

Knorre, E.P. 1953. Los' v SSSR (Elk in the USSR). Kand. Diss.

Knorre, E.P. 1956. Opytnaya loseferma (Experimental Elk Farm). Syktyvkar.

Knorre, E.P. 1957. Materialy po ekologii i znacheniyu nosoglotochnogo ovoda losya (Data on the ecology and importance of nasopharyngeal gadfly for elk). *Zool. Zhurn.*, vol. 36, no. 4.

Knorre, E.P. 1959. Ekologiya losya (Ecology of elk). *Tr. Pechoro-Ilychsk. Gos. Zapovedn.*, no. 7. Syktyvkar.

Knorre, E.P. and E.K. Knorre. 1953. Osobennosti termoregulyatsii u losya (Thermoregulation in elk). *Zool. Zhurn.*, vol. 32, no. 1.

Knorre, E.P. and E.K. Knorre. 1956. Zakonomernosti rosta i sezonnykh izmenenii zhivogo vesa losya (Growth patterns and seasonal changes in body weight of elks). *Zool. Zhurn.*, vol. 35, no. 8.

Knyazev, V. 1946. Teberdinskii gosudarstvennyi zapovednik (Teberdin State Preserve). Tbilisi.

Kolesnikov, I.M. 1950. Sluchai gibeli saigakov v Prikaspiiskoi nizmennosti zimoi 1949/50 g. (Instances of death of saiga in Cis-Caspian lowlands in the winter of 1949 to 1950). *Priroda,* no. 10.

Kolosov, A.M. 1938. Istoriya faunisticheskikh issledovanii Altaia (A history of the faunistic studies conducted in Altai). *Tr. Altaisk. Gos. Zapovedn.,* no. 1.

Kolosov, A.M. 1939. Zveri yugo-vostochnogo Altaia i smezhnoi oblasti Mongolii (Animals of southeast Altai and adjoining Mongolian region). *Uch. Zap. Mosk. Gos. Un-ta, Zool.,* no. 20.

Kolosov, A.M. 1953. Rekonstruktsiya i obogashchenie promyslovoi fauny Dal'nego Vostoka (Restoration and enrichment of game fauna of the Far East). *Tr. Mosk. Pushno-Mekhov. In-ta,* vol. 4.

Kolosovskii, R. 1884. Olen' i okhota na nego v Makar'evskom uezde Nizhegorodskoi gubernii (Deer and its hunting in Makar'ev region of Nizhegorod province). *Priroda i Okhota,* July.

Kolpakov and Vasil'ev. 1936. Kulan (Asiatic wild horse). *Konevodstvo,* no. 11.

Kolyushev, I.I. 1936. Mlekopitayushchie krainego severa zapadnoi i srednei Sibiri (Mammals of far northwestern and central Siberia). *Tr. Biol. N.-I. In-ta* (*Tomsk. Un-ta*), vol. 2.

Kolyushev, I.I. 1955. Promyslovye zveri Zakarpatskogo kraya (Game animals of Trans-Carpathian region). *Nauchn. Zap. Uzhgorodsk. Un-ta,* vol. 11. Uzhgorod.

Kompanets, V. 1958. Los' v derevne (Elk in the village). *Okhota i Okhotn. Khoz.,* no. 4.

Konoshevich, A. 1958. Brakon'ery nakazany (Poachers prohibited). *Okhota i Okhot. Khoz.,* no. 1.

Köppen, F.Th. 1883. Das vermutliche Vorkommen des Bison im Gouvernement Nishnij-Novgorod. *Beitr. z. Kennt. d. Russ. Reiches. Zweite Folge,* vol. 6. St. Petersburg.

Köppen, F.Th. 1883. Die Verbreitung des Elentiers im Europäischen Russland. *Beitr. z. Kenntn. d. Russ. Reiches. Zweite Folge,* vol. 6. St. Petersburg.

Köppen, F.Th. 1896. K istorii tarpana v Rossi (History of tarpan in Russia). *Min-vo Narodn. Prosveshch. Sed'moe Desyatiletie,* pt. 103, January.

Koptelov, A. 1925. Dikaya loshad' v Altaiskom okruge (Wild horse in Altai region). *Okhotnik i Pushnik Sibiri,* nos. 5–6.

Kopylov, I.P. 1948. Okhotnich'e khozyaistvo Irkutskoi oblasti (Game Hunting in Irkutsk District). Irkutsk.

Kopylov, I.V. 1950. Dikie kopytnye zhivotnye Irkutskoi oblasti (Wild Hoofed Animals in Irkutsk District). Irkutsk.

Korelov, M.N. 1947. O znachenii kabana v zhizni el'nikov Tyan-Shanya (Importance of wild boar in growth of Tien Shan fir plantations). *Vestn. AN Kazakhsk. SSR,* no. 3.

Korneev, O.P. 1952. Viznachnik zviriv UkSSR. Kiev (in Ukranian).

Korneev, O.P. 1953. Vikopna fauna alyuvial'nykh piskiv seredn'go Dnipra (ssavtsi). *Tr. Zool. Muzeya Kiivsk. Derzhavn. Un-ta,* no. 3 (in Ukranian).

Korochkina, L.N. 1958. Belovezhskii zubr (Belovezh wisent). *Tr. Zapovedno-Okhotnich'ego Khozyaistva Belovezhskaya Pushcha,* no. 1. Minsk.

Korsakov, A.M. 1938. Predveritel'nye dannye op faune mlekopitayushchikh trekh lesostepnykh uchastkov Naurzumskogo gos. zapovednika (Preliminary data on mammalian fauna of three forest-steppe sections of Naurzum state preserve). *Tr. Naurzumsk. Gos. Zapovedn.,* no. 1.

Koshkin, V.N. 1936. Ostrov Begicheva i ego promyslovye vozmoshnosti (Begicheva Island and its game potential). *Sov. Arktika,* no. 11.

Koshkin, V.N. 1937. Nekotorye dannye po promyslovoi faune ostrova Begicheva (Some data on game fauna of Begicheva Island). *Probl. Arktiki,* no. 2.

Koshkin, V.V. 1952. Los' v Ul'yanovskoi oblasti (Elk in Ul'yanov region). *Priroda*, no. 1.

Kostarev, A. 1957. Spasli losya (Elk have been rescued). *Okhota i Okhot. Khoz.*, no. 2.

Kostin, V.P. 1955. Materialy po ekologii i promyslovomu znacheniyu dzheirana (Material on the ecology and game significance of goitered gazelle). *Tr. In-ta Zoologii AN Kazakhsk. SSR*, vol. 4.

Kotlyarova, Kh., I. Taran, E. Zamakhaeva, A. Chekomasova and A. Polyakova. 1957. Izuchenie roli dikikh zhivotnykh v epizootologii brutselleza koz'eovech'ego tipa (Study of the role of wild animals in the epizooty of brucellosis in goats and sheep). *Tez. Dokl. Konfer. po Prirodnoi Ochagovosti i Epidemiologii*. Saratov.

Kotov, V.A. 1958. Pitanie rysi v Kavkazskom zapovednike (Feeding of lynx in Caucasian preserve). *Tr. Kavkazsk. Gos. Zapovedn.*, no. 4. Maikop.

Kotovshchikova, M. 1936. Materialy po uchetu i biologii krymskogo blagorodnogo olenya (Data on population counts and biology of Crimean red deer). Sb. Krymskogo Gos. Zapovedn., no. 1) (*Nauchn. Trudy Gos. Zapovednikov*, ser. 2).

Kovács, G. and J. Kovács. 1957. Jelentös Vadbetegségek a Bükkhegységben. *Erdö*, köt. 6, no. 2. Budapest.

Kozhamkulova, B.S. 1957. Iskopaemye mlekopitayushchie antropogna Kazakhstana po kollektsiyam kraevedcheskikh muzeev respubliki (Fossilized anthropogen mammals of Kazakhstan from collections of regional museums in the republics). *Izv. AN Kazakhsk. SSR, Ser. Biol.*, no. 2 (14).

Kozhanchikovy, L. and I. Kozhanchikovy. 1924. Promyslovaya okhota i rybolovstvo v Minusinskoi taiga (Game hunting and fishing in Minusinsk taiga). *Ezhegod. Gos. Muzeya im. Mart'yanova*, vol. 2, no. 2. Minusinsk.

Kozlov, V.V. 1947. Kolichestvennyi uchet kopytnykh v Mordovskom zapovednike (Numerical population counts of hoofed animals in Mordov preserve). *Nauchn.-Metod. Zap. Gl. Upr. po Zapovedn.*, no. 9.

Kozlov, V.V. 1953. Nekotorye itogi bor'by s volkami v gosudarstvennykh zapovednikakh (Some results of control of wolves in state preserves). Sb. *Preobrazovanie Fauny Pozvonochnykh Nashei Strany* (*Biotekhnicheskie Meropriyatiya*). Moscow.

Kozlov, V.V. 1954. Vliyanie zapovednogo rezhima na faunu mlekopitayushchikh Meshcherskoi nizmennosti (Effect of preserve regime on mammalian fauna of Meshcher lowland). *Zool. Zhurn.*, vol. 33, no. 4.

Kozlova-Pushkareva, E.V. 1933. Ptitsy i promyslovye mlekopitayushchie Vostochnogo Kenteya (Birds and game mammals of eastern Kentei). *Tr. Mongol'sk. Komissi,* no. 10. Moscow-Leningrad.

Krainova, L.V. 1947. Vosstanovlenie zubra na Kavkaze (Restoration of wisent in the Caucasus). Sb. *20 Let Kavkazsk.Gos.Zapovednika.* Moscow.

Krainova, L.V. 1951. Pitanie zubrov Kavkazsk. gos. zapovednika (Feeding of wisent in Caucasian state preserve). *Byull. Mosk. Obva Ispyt. Prirody, Otd. Biol.,* vol. 56, no. 6. Moscow.

Krammer, H. 1957. Der Gemsen Kindergarten. *Kosmos* (*BRD*), vol. 53, no. 4. Stuttgart.

Krashennikov, S.P. 1786. Opisanie zemli Kamchatki (Description of Kamchatka Land). St. Petersburg, 2nd printing.

Krasovskii, 1858. Oblast' Sibirskikh Kirgizov. Ch. 1–3 (Siberian Kirgizia region. Pts. 1 to 3). *Mater. Dlya Geografii i Statistiki Rossii.* St. Petersburg.

Krasovskii, V.P. 1955. Prikhod losei v Khoperskii zapovednik (Arrival of elk in Khoper preserve). *Priroda,* no. 1.

Kravchenko, V. and E. Shcherbina. 1957. Kulan v Badkhyze (Kulan in Badkhiz). *Okhota i Okhot. Khoz.,* no. 8.

Kreps, G. 1928. Dikii severnyi olen' na Kol'skom poluostrove i proekt organizatsii Laplandskogo zapovednika (Wild reindeer in Kola Peninsula and the project for organization of Lapland preserve). *Karelo-Murmanskii Krai,* nos. 10–11. Leningrad.

Krivosheya, N.V. 1884. Zametski o Novo-Zemel'noi faune (Notes on Novaya Zemlya faune). *Priroda i Okhota,* November.

Kröning, F. and F. Vorreyer. 1957. Untersuchungen über Vermehrungsraten und Körpergewichte beim weiblichen Rotwild. *Zeitschr. f. Jagdwiss.,* vol. 3, no. 4. Hamburg.

Krott, P. 1956. Zur Aufzucht der Eichkälbern. *Zeitschr. f. Jagdwiss.,* vol. 2, no. 1. Hamburg.

Krumbiegel, J. 1954. *Biologie der Säugetiere,* vol. 1.

Krylov, P.N. 1926. Visherskii Krai. (Zametki iz puteshest vii po Permskoi gubernii v 1870–1878 gg.) [Vysher region (Notes from travels in Perm province from 1870 to 1878)]. *Ural, Tekhniko-Ekon. Sb.,* no. 8, *Ural'skii Sever,* pt 1. Sverdlovsk.

Kuchin, A. 1958. Losi pod Biiskom (Elk around Biisk). *Altaisk. Pravda.* Barnaul, May 25.

Kuklin, S.A. 1946. Losi Molotovskoi oblasti (Elk of Molotov District).

Kuklin, S.A. 1951. Okhota v Molotovskoi oblasti v proshlom i nastoyashchem (Hunting in Molotov district in the past and at present). Sb. *Na Zapadnom Urals.* Molotov.

Kulagin, N. 1919. Zubry Belovezhskoi Pushchi (Belovezh Forest wisent). Moscow.

Kulagin, N.M. 1932. Losi SSSR (Elk of the USSR). *Tr. Labor. Priklad. Zoologii AN SSSR.*

Kulagin, N.M. 1940. Fauna BSSR. T. 1. Mlekopitayushchie, vyp. 4. Kopytnye (Fauna of Belorussian Soviet Socialist Republic, vol. 1: Mammals; no. 4: Ungulates). Minsk.

Kul'pin, P.I. 1954. Dzheirany i saiga v pustnye Betpak-Dala (Goitered gazelle and saiga in Betpak-Dala desert). *Priroda,* no. 4.

Kurapova, M. and P. Stepanov. 1940. Pyatnistye oleni v Teberdinskom zapovednike (Sika in Teberdin preserve). *Sov. Okhotnik,* no. 10.

Kurazhskovskii, Yu.N. 1949. Dikii severnyi olen' v Komi ASSR i prilegayushchikh raionakh (Wild reindeer in Komi Autonomous Soviet Socialist Republic and adjacent regions). *Okhrana Prirody,* vol. 7.

Kurazhskovskii, Yu.N. 1949. Ob adaptatsii dikikh kopytnykh k izmeneniyam landshafta, sozdannym deyatel'nost'yu cheloveka (Adaptation of wild ungulates to topographic changes brought about by human activity). *Zool. Zhurn.,* vol. 28, no. 2.

Kurazhskovskii, Yu.N. 1950. Akklimatizatsiya marala v Bashkirskom zapovednike (Acclimatization of maral in Bashkir preserve). *Okhrana Prirody,* vol. 10.

Kurazhskovskii, Yu.N. 1952. K izucheniyu ekologii kosuli v lesnykh nasazhdeniyakh zasushlivykh oblasti (Study of the ecology of roe deer in forest plantations of arid zones). *Okhrana Prirody,* vol. 15.

Kuznetsov, B.A. 1937. Zametki o faune mlekopitayushchikh Alaiskoi doliny (Notes on mammalian fauna of Alai valley). *Byull. Mosk. Ob-va Ispyt. Prirody, Otd. Biol.,* vol. 46, no. 2.

Kuznetsov, B.A. 1948. Mlekopitayushchie Kazakhstana (Kazakhstan Mammals). Moscow.

Kuznetsov, B.A. 1948. Zveri Kirgizii (Kirgizian animals). *Mater. k Poznan. Fauny i Flory SSSR, Nov. Ser., Otd. Zool.,* no. 12, p. 27.

Kuznetsov, B.A. 1952. Fauna mlekopitayushchikh Moldavii (Mammalian fauna of Moldavia). *Izv. Moldavsk. Fil. AN SSSR,* nos. 4–5, pp. 7–8.

Kuznetsov, B.A. 1954. Materialy po faune mlekopitayushchikh Latviiskoi SSR (Mammalian fauna of Latvian Soviet Socialist Republic). *Byull. Mosk. Ob-va Ispyt. Prirody, Otd. Biol.,* vol. 59, no. 4.

Lamberti, Archangelo. 1654. Relatione della Colchide hoggi detta Mengrellia, hella quale si tratta dell'origine. Costumi e Cosi naturali di quei Paesi, Napoli (Russian translation by P. Yurchenko: *Zap. Odessk. Ob-va Ist. i Drevnostei,* vol. 10, 1877; and K.F. Gana: *Sb. Mater. Dlya Opisaniya Mestn. i Plemen Kavkaza,* no. 43, 1913).

Laptev, I.P. 1955. O rasprostranenii nekotorykh mlekopitayushchikh v Zapadnoi Sibiri (Distribution of some mammals in western Siberia). *Zametki po Faune i Flore Sibiri,* no. 18. Tomsk.

Laptev, I.P. 1958. Mlekopitayushchie taezhnoi zony Zapadnoi Sibiri (Mammals of Western Siberian Taiga Zone). Tomsk.

Laptev, M.K. 1929. Opredelitel' mlekopitayushchikh Srednei Azii (Identification of Mammals of Middle Asia). Tashkent, no. 1.

Laptev, M.K. 1934. Materialy k poznaniyu fauny pozvonochnykh Turkmenistana (Data on fauna of Turkmenian vertebrates). *Izv. Turkmensk. Mezhduvedomstv. Komiteta po Okhrane Prirody i Razvitiyu Prirodn. Bogatstv.,* no. 1. Ashkhabad.

Laptev, M.K. 1936. Opyt bioucheta okhot-promyslovykh zhivotnykh tsentral'nogo Kopet-Daga (Turkmenskoi SSSR) [Live counts of game-hunting animals of central Kopet-Dag (Turkmenian Soviet Socialist Republic)]. *Byull. Turkmensk. Zool. Stants.,* no. 1. Ashkhabad.

Larin, V. 1958. Los' prishel v gorod (The elk has come to town). *Okhota i Okhot. Khoz.,* No. 11.

Lavrov, N.P. 1929. Geograficheskoe raspredelenie, biologiya i khozyaistvennoe znachenie kosuli v SSSR (Geographic distribution, biology, and economic importance of roe deer in the USSR). *Tr. po Lesn. Opytn. Delu Tsentr. Lesn. Opytn. Stants.,* no. 6.

Lavrov, N.P. 1954. Akklimatizatsiya promyslovykh zverei SSSR (Acclimatization of game animals of the USSR). *Priroda,* no. 3.

Lavrovskii, A.A. 1950. Morfologicheskie osobennosti, ekologiya i promyslovoe znachenie kabana del'ty Volgi (Morphological characteristics, ecology, and game significance of wild boar of Volga delta). Kand. Diss.

Lavrovskii, A.A.1950. O vliyanii letnei zasukhi i surovoi zimy 1949/50 g. na chislennost' i razmeshchenie saigakov (Effect of summer droughts and the severe winter of 1949 to 1950 on the population number, and distribution of saiga). *Okhrana Prirody,* vol. 10.

Lebedeva, L.S. 1956. Ekologicheskie osobennosti kabana Belovezhskoi Pushchi (Ecological peculiarities of wild boar in Belovezh Forest). *Uch. Zap. Mosk. Bor. Ped. In-ta im. V.P. Potemkina,* vol. 61, *Zoologiya,* nos. 4–5.

Lebedeva, L.S. 1956. O sostave letnikh kormov kabana v vysokogornoi zone Kavkazskogo zapovednika (Composition of summer food of wild boar in high montane zone of Caucasian preserve). *Uch. Zap. Mosk. Gor. Ped. In-ta im. V.P. Potemkina,* vol. 61, *Zoologiya,* nos. 4–5.

Leble, B.B. 1953. Pushnye zveri Arkhangel'skoi oblasti (Fur-bearing Animals of Arkhangelsk District). Arkhangelsk.

Leisewitz, W. 1906. Über Steinböcke aus dem Zentralen Tien-Shan. *Zool. Anz.*, vol. 29.

Lengrecken, H. 1953. Der Ur und seine Beziehungen zum Menschen. *Die neue Brehm-Bücherei.* Wittenberg-Lutherstadt.

Lengrecken, H. 1955. Ur, Hausrind und Mensch. *Deutsche Ak. d. Landwirtschaftswissensch., Wissensch. Abhandl.,* no. 14/1955. Berlin.

Lentovskii, M.P. 1928. K voprosu obitaniya i okhrany kosulei v b. Kokchetavskom uezde (Habitation and preservation of roe deer in the former Kokchetav district). *Okhotnik,* no. 9.

Leont'ev, A.N. 1949. Okhotnichii promysel (Game hunting). *Tr. Kyakhtinsk. Kraevedchesk. Muzeya i Kyakhtinsk., Otd. Vses. Geograf. Ob-va,* vol. 16. Ulan-Ude.

Lepekhin, I.I. 1821. Dnevnye zapiski puteshestviya po raznym provintsiyam Rossiiskogo gosudarstva v 1768 i 1769 gg. Ch. 1 (Daily Records of Travels in Different Provinces of the State of Russia in 1768 and 1769, pt. 1). St. Petersburg.

Levchenko, M. 1882. Ischeznuvshie i ischezayushchie v Yuzhnoi Rossii zhivotnye (Extinct and vanishing animals in southern Russia). *Kievskaya Starina,* vol. 3.

Leviev, P. 1939. Okhotnich'i i promyslovye zveri i ptitsy Saryassiiskogo raiona (Hunting and game animals and birds of Sary-Assiya region). *Tr. Uzbek. Zool. Sada,* vol. 1. Tashkent.

Lezhnin, P.D. 1922. Bogatstva Priamur'ya i Zabaikal'ya (Resources of Amur and Trans-Baikal). Chita.

Likhachev, A.I. 1955. Razmnozhenie i embrional'noe razvitie losya (Reproduction and embryonic growth of elk). *Tr. Tomsk. Gos. Un-ta,* no. 131.

Likhachev, A.I. 1956. Prisposobitel'nye morfo-funktsional'nye osobennosti v sisteme organov dvizheniya losei (Adaptive morpho-functional characteristics of locomotory organs of elk). *Zool. Zhurn.,* vol. 35, no. 3.

Likhachev, G.N. 1937. Zametki o faune goszapovednika "Tul'skie zaseki" (Notes on the fauna of Tula preserve). *Tr. po Lesn. Opytn. Delu Tul'skikh Zasek,* no. 1.

Likhachev, G.N. 1939. Materialy po pitaniyu losya drevesnymi kormami v Tul'skikh zasekakh (Materials on elk feeding on arboreal foods in Tul'sk sector). *Tr. po lesn. opytn. Delu Tul'skikh Zasek.,* No. 3.

Likhachev, G.N. 1957. Nekotorye dannye po pitaniyu losya v Tul'skikh dubravakh (Some data on feeding of elk in Tula oak groves). *Zool. Zhurn.,* vol. 36, no. 12.

Ling, Kh.I. 1955. Izmeneniya v rasprostranenii kabana v Sovetskoi Pribaltike za poslednee stoletie (Variations in distribution of wild boar in Soviet Baltics in the last century). *Ezhegod. Ob-va Estest-voisp. Pri AN Estonsk. SSR,* vol. 48.

Ling, Kh.I. 1958. Fauna Estonii (Estonian fauna). *Okhota i Okhot. Khoz.,* no. 3.

Linke, W. 1957. Der Rothirsch. *Die neue Brehm-Bücherei.* Wittenberg-Lutherstadt.

Lobachev, S.V. 1930. Obzor okhotnich'ikh promyslov Vyatskogo kraya (A review of game animals of Vyats region). *Tr. po Lesn. Opytn. Delu Tsentr. Lesn. Opytn. Stants.,* no. 7.

Lobachev, S.V. 1932. Verkhne-Vychegodskii raion (Verkhne-Vychegda region). Sb. *Verkhne-Vychegodskaya Ekspeditsiya.* Moscow.

Loginov, V.V. 1936. Novye dannye k poznaniyu biologii kavkazskogo kabana (Recent data on the biology of Caucasian wild boar). *Byull. Mosk. Ob-va Ispyt. Prirody. Otd. Biol.,* vol. 45, no. 1.

Lopyrin, A.I., N.V. Loginova and A.P. Inyakova.1956(1957), *Byull. Nauch. Tekhn. Inform. Vses. In-ta Ovtsevodstva i Khozovodstva,* no. 3 (25).

Lorents, F. 1881. Moskovskie zametki (Moscow notes). *Priroda i Okhota,* vol. 2, April.

Lorenz von Liburnau, L. 1907. Zur Kenntniss der Steinböcke Innerasiens. *Denkschr. d. Kais. Akad. d. Wiss. Math.-Naturwiss. Kl,* vol. 80. Wien.

Loukashkin, A.S. and V.N. Jernakov. 1934. Fur trade in north Manchuria. *The China Journ.,* vol. 21, nos. 5–6.

Lukashkin, A.S. [Loukashkin, A.S.]. 1927. Mongol'skaya stepnaya antilopa "Dzeren" (Mongolian steppe antelope). *Tr. Ob-va Izuch. Man'chzhursk. Kraya, Zoologiya,* no. 1. Kharbinsk [Harbin].

Lukashkin, A.S. [Loukashkin, A.S.]. 1934. Urkichikhanskaya kontsessiya (Urkichikhansk concession). *Vestn. Man'chzhurii,* no. 7. Kharbinsk [Harbin].

Lyakhov, S.M. and Yu.P. Rukhlyadev. 1952. Okhotnich'e-promyslovye ptitsy i zveri Kuibyshevskoi oblasti (Game Birds and Animals of Kuibyshev District). Kuibyshev.

Lydekker, R. 1898. *Wild Oxen, Sheep, and Goats of All Lands.* London.

Lydekker, R. 1912. *The Ox and Its Kindred.* London.

Lydekker, R. 1913–1916. *Catalogue of Ungulate Mammals in the British Museum (Nat. History).* London, vol. 1, 1913; vols. 2 and 3, 1914; vol. 4, 1915; and vol. 5, 1916.

Maak, R. 1859. Puteshestvie na Amur (Amur Travels). St. Petersburg.

Maak, R. 1861. Puteshestvie po doline r. Ussuri (Ussuri River Valley Travels). St. Petersburg, vol. 1.

Machul'skii, S.N. 1941. Gel'mintozy dzerana (*Gazella gutturosa*) [Helminthiasis of Mongolian gazelle (*Gazella gutturosa*)]. *Tr.*

Buryat-Mongol'sk. Zootvet. In-ta, vol. 2. Ulan-ude.

Maidel', G. 1894. Puteshestvie po severo-vostochnoi chasti Yakutskoi oblasti v 1868–1880 g. (Travels in northeastern part of Yakutia from 1868 to 1880). *Zap. Ak. Nauk,* vol. 74, Appendix, no. 3. St. Petersburg.

Makarov, V.N. 1949. Okhrana prirody v SSSR (Conservation of Nature in the USSR). Moscow.

Makridin, V.P. 1955. Losi v tundrakh Evropeiskogo Severa (Elk in the tundras of northern Europe). *Priroda,* no. 1.

Malenkov, I.I. 1958. O rasprostranenii dzheirana i shakala v Ferganskoi doline (Distribution of goitered gazelle and jackal in Ferghana valley). *Zool. Zhurn.,* vol. 37, no. 4.

Malyshev, K.G. 1958. Opyty degel'mintizatsii losei (Experiments on dehelminthization of elk). *Izv. Irkutsk. S.-Kh. In-ta,* no. 8 (*F-Ta Zootekhn. i Okhotoved.*). Irkutsk.

Mambetzhumaev, A. 1955. Biologiya dzheirana (Biology of goitered gazelle). Kand. Diss.

Manteifel', P.A. 1934. Odomashnivanie losei (predvaritel'n. soobshch.) [Domestication of elk (Preliminary report)]. *Byull. Zooparkov i Zoosadov,* no. 8.

Marikovskii, P.I. 1953. Sposoby i ob''ekty okhoty po motivam naskal'nykh risunkov Chulakskikh gor (Kazakhskaya SSR) [Methods and objects of hunting deciphered from rock drawings in Chulak mountains (Kazakh Soviet Socialist Republic)]. *Zool. Zhurn.,* vol. 32, no. 6.

Markgraf, O. 1876. Usloviya okhoty i okhotnich'ego promysla v Chernomorskom okruge Kavkaza (Conditions of hunting and game husbandry in Black Sea region of the Caucasus). *Okhota,* no. 2.

Markov, E.A. and L.L. Mlokosevich. 1935. Zakatal'skii zapovednik (Zakatal'sk Preserve). Baku.

Markov, E.L. 1932. Dikie svin'i Zakavkaz'ya (Wild boar of Trans-Caucasus). Tiflis.

Markov, E.L. 1934. Okhotnich'e khozyaistvo Zakavkaz'ya (Game Hunting in Trans-Caucasus). Tiflis.

Markov, E.L. 1938. Okhotnich'e-promyslovye zhivotnye Lagodekhskogo zapovednika (Game Animals of Lagodekh preserve). Tbilisi.

Martynov, N.M. 1955. Losi nizhnego Povolzh'ya (Elk of Lower Volga). *Priroda,* no. 9.

Martynov, P.M. 1959. Losi v Saratovskoi oblasti (Elk in Saratov district). *Okhrana Prirody,* vol. 13.

Marvin, M.Ya. 1950. Promyslovye zveri i ptitsy Karelo-Finskoi SSR (Game Animals and Birds of Karelia-Finsk Soviet Socialist Republic). Petrozavodsk.

Marvin, M.Ya. 1951. Zhivotyi mir Karelo-Finskoi SSR (Fauna of Karelia-Finsk Soviet Socialist Republic). Petrozavodsk.

Masal'skii. 1913. Turkestanskii Krai (Turkestan territory). *Rossiya.* St. Petersburg.

Mashkovtsev, A.A. 1940. Okhota v gorakh Tyan'-Shanya (Hunting in the mountains of Tien-Shan). *Boets-Okhotnik,* no. 7.

Mashkovtsev, A.A. 1940. Sayanskii dikii reliktovyi severnyi olen' (Sayan wild relict reindeer). *Dokl. AN SSSR, Nov. Ser.,* vol. 27 no. 1.

Matyushin, A.I. 1950. Akklimatizatsiya pyatnistogo olenya pod Moskovoi (Acclimatization of sika around Moscow). *Tr. Mosk. Pushno-Mekh. In-ta,* vol. 5.

McCann, L.J. 1956. Ecology of mountain sheep. *Amer. Midland Natur.,* vol. 56, no. 2. Notre Dame.

McHugh, T. 1958. Social behavior of American buffalo (*Bison bison bison*). *Zoologica* (USA), vol. 43, pt. 1, no. 1. New York.

Meier, L. 1794. Povestvennoe, zemlemernoe i estestvennoe opisanie Ochakovskoi zemli (Folklore and Geodetic and Natural Description of Ochakov Land). St. Petersburg.

Meier, L. 1865. Opisanie Kirgizskoi stepi Orenbyrgskogo vedomstva (Description of Kirgizian steppes, Orenburg division). *Mater. Dlya Geografii i Statistiki Rossii.* St. Petersburg.

Meklenburtsev, R.N. 1936. Materialy po mlekopitayushchim i ptitsam Pamira (Data on mammals and birds of Pamir). *Tr. Sr.-Az. Gos. Un-ta, Ser.* VIIIa, *Zoologiya,* no. 22.

Meklenburtsev, R.N. 1937. Materialy po faune ptits i mlekopitayushchikh khrebta Nura-Tau (Data on the bird and mammalian fauna of Nura-Tau range). *Tr. Sr.-Az. Gos. Un-ta, Ser.* VIIIa, *Zoologiya,* no. 26.

Meklenburtsev, R.N. 1948. Pamirskii arkher *Ovis polii polii* Blyth. [Pamir argali sheep (*Ovis polii polii* Blyth.)]. *Byull. Mosk. Ob-va Ispyt. Prirody Otd. Biol.,* vol. 53, no. 5.

Meklenburtsev, R.N. 1949. K ekologii sibirskogo gornogo kozla na Pamire (Ecology of Siberian ibex in Pamir). *Zool. Zhurn.,* vol. 23, no. 5.

Meklenburtsev, R.N. 1958. Materialy po nazemnym pozvonochnym basseina r. Kashka-Dar'i (Data on the land vertebrates of Kashka-Darya River basin). *Tr. Sr.-Az. Gos. Un-ta, Nov. Ser.,* no. 130, *Biol. Nauk.,* vol. 30.

Melander, V.A. 1938. Opredelitel' mlekopitayushchikh Smolenskoi i smezhnykh oblasti (Identification of Mammals of Smolensk and Adjacent Districts). Smolensk.

Mel'nikova, T.G. 1953. Iksodovye kleshchi dikikh i domashnikh zhivotnykh Krymskogo zapovendika (Ixode mites of wild and domestic animals of Crimean preserve). *Zool. Zhurn.*, vol. 32, no. 3.

Menard, G.A. 1930. Pantovoe khozyaistvo (Velvet Antler Farming). Moscow-Leningrad.

Ménétriés, E. 1832. *Catalogue raisonnée des objets de zoologie recueillis dans un voyage du Caucase et jusqu'aux frontières actuelles de la Perse.* St. Petersburg.

Mertts, P.A. 1951. Oleni Voronezhskogo zapovednika i okrestnykh leskhozov (Deer of Voronezh preserve and neighboring forests). *Byull. Mosk. Ob-va Ispyt. Priordy. Otd. Biol.*, vol. 56, no. 5.

Mertts, P.A. 1953. Ekologiya evropeiskogo olenya v usloviyakh Usmanskogo lesnogo massive (Ecology of European deer under Usmansk forest massif conditions). Kand. Diss.

Mertts, P.A. 1953. Rol' zheludei v kormovom balanse olenei Voronezhskogo zapovednika (Role of acorns in the food balance of deer in Voronezh preserve). *Tr. Voronezhsk Gos. Zapovedn.*, no. 4. Voronezh.

Mertts, P.A. 1954. O povyshenii poligamii u olenei v okhotnich'em khozyaistve i pantovo-olenevodcheskikh sovkhozakh (Increase in polygamy of deer in game farms and velvet antler farms). *Tr. Voronezhsk. Gos. Zapovedn.*, no. 5. Voronezh.

Mertts, P.A. 1957. Rol' snezhnogo pokrova v zhizni olenei voronezhskoi populyatsii (Role of snow cover in the life of Voronezh deer population). *Tr. Voronezhsk. Gos. Zapovedn.*, no. 7. Voronezh.

Meyer-Holzapfel, M. 1958. Bouquetins en captivité. *Mammalia,* vol. 22, no. 1. Paris.

Middendorff, A.Th. 1851. *Zoologie. Säugethiere, Vogel und Amphibien. Reisen im äussersten Norden und Osten Sibiriens Während der Jahre 1843 und 1844* . . . . St. Petersburg, vol. 2, pt. 2.

Middendorff, A.Th. 1867. Die Thierwelt Sibiriens, *Sibirische Reise,* vol. 4, pt. 2. Erste Lieferung, St. Petersburg.

Middendorff, A.Th. 1869. Sibirskaya fauna. Puteshestvie na sever i vostok Sibiri (Siberian fauna. Travels in Northern and Eastern Siberia). St. Petersburg, pt. 2, sect. 5.

Middendorff, A.Th. 1874. Die Thierwelt Sibiriens, *Sibirishche Reise,* vol. 4, pt. 2. Zweite Lieferung, St. Petersburg.

Migulin, O. 1927. Shkidni ta korisni zviri Ukraini. Kharkov [in Ukranian].

Migulin, O. 1929. Viznachnik zviriv Ukraini. Kharkov [in Ukranian].

Migulin, O. 1938. Zviri UkRSR. Kiev [in Ukranian].

Mikhailov, A. 1868. Ocherki prirody i byta Belmorskogo Kraya Rossii (Description of the nature and living conditions of the White Sea region of Russia). *Okhota v Lesakh Arkhangel'skoi Gub.* St. Petersburg.

Mikheev, A.V. 1948. Okhotnich'i bogatstva Eniseisko-Pyasinskoi tundry (Game riches of Yenisey-Pyasina tundra). *Okhrana Prirody,* vol. 4.

Mikhel', N.M. 1937. Ocherki promyslovoi okhoty v severo-vostochnoi Yakutii (Outline of game hunting in northeast Yakutia). *Arctica,* vol. 5.

Miller, G.S. 1912. *Catalogue of Mammals of Western Europe.* London.

Miller, G.S. and R. Kellog. 1955. List of North American Recent mammals. *U.S. Nat. Mus. Bull.,* no. 205. Washington.

Minervin, V.M. 1944. O vodopoino-pastbishchnom rezhime dzheiranov i ovets v pustyne (Water-hole pasture regime of goitered gazelle and sheep in the desert). *Tr. Turkmensk. Fil. AN SSSR,* no. 5.

Minervin, V.N. 1955. Pastbishchno-vodopoinyi rezhim ovets v pustyne (Pasture-Water-Hole Regime of Sheep in the Desert). Ashkhabad.

Mirolyubov, I.I. and L.P. Ryashchenko, 1948. Pyatnistyi olen' (Sika). Vladivostok.

Mishin, I.P. 1952. Dikii severnyi olen' Sakhalina (Wild reindeer of Sakhalin). *Priroda,* no. 1.

Mishin, I.P. 1954. Zarazhennost' severnykh olenei ostrova Sakhalina nosovym ovodom v zavisimosti ot razvitiya vibris (Infection of Sakhalin Island reindeer by nasal gadfly in relation to growth of vibrissae). *Zool. Zhurn.,* vol. 33, no. 1.

Mitskevich, Yu. Yu. 1958. K rasshifrovke tsikla razvitiya nematody *Elaphostrongylus rangiferi* sp. nov. ot severnogo olenya (Study of the life cycle of nematode *Elaphostrongylus rangiferi* sp. nov. in reindeer). *Dokl. AN SSSR,* vol. 119, no. 3.

Mlokosevich, L.F. 1894. Prichiny ischeznoveniya poleznykh zhivotnykh i mery bor'by s etim zlom (Factors responsible for the extinction of wild animals and measures for combating this evil). *Kavkazsk. Sel'skoe Khozyastvo,* nos. 26–27. Tiflis.

Mohr, E. 1952. Der Wisent. Die neue Brehm-Bücherei. Wittenberg-Lutherstadt.

Moisan, G. 1957. Late breeding in moose (*Alces alces*). *J. Mammal.,* vol. 25, no. 1.

Moisan, G. 1957. Le caribou de Gaspe. III. Analyse de la population et plan d'amenagement. *Naturaliste Canad.,* vol. 84, no. 1. Quebec.

Molodykh, I.F. 1931. Puti svyazi i snabzhenie Kolymako-Indigirskogo kraya (Communication and supply lines in Kilyma-Indigirsk region). Sb. *Mater. Partii po Issledovaniyu r. Kolymy,* no. 5. Irkutsk.

Morits, L. 1930. Bezoarovyi kozel v Turkmenii (Bezoar goat in

Turkmenia). *Okhotnik,* no. 11.

Morits, L. 1931. Kopet-dagskii baran v Turkmenii (Kopet-Dag sheep in Turkmenia). *Okhotnik,* nos. 5–6.

Murie, A. 1944. The *Wolves of Mount McKinley.* Washington.

Murie, O.J. 1957. *Elk of North America.* Washington, 2nd print.

Naniev, V.I. 1956. Kavkazskii zubr-dombai (Caucasian Dombai wisent). *Uch. Zap. Severo-Osetinsk. Gos. Ped. In-ta,* no. 20. Ordzhonikidze.

Naryshkin, D. 1900. Okhota na losei (Elk Hunting). St. Petersburg.

Nasimovich, A.A. 1938. K poznaniyu mineral'nogo pitaniya dikikh zhivotnykh Kavkazskogo zapovednika (Study of the mineral food of wild animals of Caucasian preserve). *Tr. Kavkazsk. Gos. Zapovedn.,* vol. 1.

Nasimovich, A.A. 1938. Vliyanie lavin na rastitel'nyi i zhivotnyi mir Kavkazskogo zapovednik (Effect of avalanches of fauna and flora of Caucasian preserve). *Priroda,* nos. 7–8.

Nasimovich, A.A. 1939. Zima v zhizni kopytnykh Zapadnogo Kavkaza (Winter in the life of west Caucasian ungulates). Sb. *Voprosy Ekologii i Biotsenoi,* no. 7.

Nasimovich, A.A. 1940. Letnie korma blagorodnogo olenya na Zapadnom Kavkaze (Summer food of red deer in western Caucasus). *Nauchn.-Metod. Zap. Gl. Upr. po Zapovedn.,* no. 7.

Nasimovich, A.A. 1940. Sezonnye migratsii i nekotorye drugie osobennosti biologii burogo medvedya na Zapadnom Kavkaze (Seasonal migrations and some other characteristics of the biology of brown beer in western Caucasus). *Nauchn.-Metod. Zap. Gl. Upr. po Zapovedn.,* no. 7.

Nasimovich, A.A. 1941. K metodike kolichestvennogo ucheta blagorodnogo olenya v Kavkazskom zapovednike (Method for census of red deer in Caucasian preserve). *Nauchn.-Metod. Zap. Gl. Upr. po Zapovedn.,* no. 8.

Nasimovich, A.A. 1941. Kolichestvennyi uchet sern i dinamika ikh pogolov'ya v Kavkazskom zapovednike (Census of chamois and its population dynamics in Caucasian preserve). *Nauchn.-Metod. Zap. Gl. Upr. po Zapovedn.,* no. 8.

Nasimovich, A.A. 1948. Novye dannye po ekologii rosomakhi v Laplandskom zapovednike (Recent data on ecology of wolverine in Lapland preserve). *Tr. Laplandsk. Gos. Zapovedn.,* no. 3.

Nasimovich, A.A. 1949. Novye dannye po biologii serny na Zapadnom Kavkaze (Recent data on the biology of chamois in western Caucasus). *Tr. Kavkazsk. Gos. Zapovedn.,* no. 3.

Nasimovich, A.A. 1949. Ocherk ekologii zapadnokavkazskogo tura (Outline of ecology of western Caucasian tur). *Tr. Kavkazsk. Gos. Zapovedn.,* no. 3.

Nasimovich, A.A. 1949. Promyslovye zveri tsentral'nogo Altaia (Game animals of central Altai). Sb. *Pushnye Bogatstva SSSR,* no. 1. Moscow.

Nasimovich, A.A. 1950. Ob organizatsii zapovednika vysokogornoi prirody Tsentral'nogo Kavkaza (Organization of a preserve in the environs of high mountains of central Caucasus). *Okhrana Prirody,* vol. 11.

Nasimovich, A.A. 1955. Rol' rezhima snezhnogo pokrova v zhizni kopytnykh zhivotnykh na territorii SSSR (Role of snow cover regime in the life of ungulates within USSR territory). *Izd. AN SSSR.* Moscow.

Nasimovich, A.A. and O.I. Semenov-Tyan-Shanskii. 1951. Pitanie burogo medvedya i otsenka ego roli kak khizhchnika v Laplandskom zapovednike (Food of brown bear and evaluation of its role as a predator in Lapland preserve). *Byull. Mosk. Ob-va Ispyt. Prirody, Otd. Biol.,* vol. 56, no. 4.

Nasimovich, A.A. and V.Ya. Rudanovskii. 1955. Zagotovka myasa dikikh zhivotnykh (Dressing of Meat of Wild Animals). Moscow-Leningrad.

Nasonov, N.V. 1923. Geograficheskoe rasprostranenie dikikh baranov Starogo Sveta (Geographic Distribution of Wild Sheep of the Old World). St. Petersburg.

Nasonov, N.V. and V.Ch. Dorogostaiskii. 1915. Dikie barany (*Ovis nivicola potanini*) Yablonovogo khrebta [Wild sheep (*Ovis nivicola potanini*) of Yablonovyi range]. *Izv. Akad. Nauk,* VI ser., vol. 9, no. 15.

Naumov, N.P. 1930. Promyslovye mlekopitayushchie Turukhanskogo kraya (Game mammals of Turukhansk region). *Sov. Sever.,* no. 3.

Naumov, N.P. 1933. Dikii severnyi olen' (Wild Reindeer). Moscow.

Naumov, N.P. 1934. Mlekopitayushchie Tunguskogo okruga (Mammals of Tunguska region). *Tr. Polyarn. Komissii AN SSSR,* no. 17.

Naumov, S.P. 1931. Mlekopitayushchie i ptitsy Gydanskogo poluostrova (Severo-zapadnaya Sibir') [Mammals and birds of Gydansk Peninsula (northwest Siberia)]. *Tr. Polyarn. Komissii AN SSSR,* no. 4.

Naumov, S.P. and I.P. Lavrov. 1948. Biologiya promyslovykh zverei i ptits SSSR (Biology of Game Animals and Birds of the USSR). Moscow.

Niezabitowski, E. 1934. Bericht über die Säugetiere Polens und ihre geographische Verbreitung. *Zeitschr. f. Säugetierk.,* vol. 9. Berlin.

Nikol'skii, A.M. 1883. Puteshestvie v Altaiskie gory letom 1882 g.

(Travels in Altai mountains in the summer of 1882). *Tr. SPb. Ob-va Estestvoisp.*, vol. 14, no. 1.

Nikol'skii, A.M. 1887. O faune pozvonochnykh zhivotnykh dna Balkhashskoi kotloviny (Vertebrate fauna of Balkhash depression). *Tr. SPb. Ob-va Estestvoisp.*, vol. 19.

Nikol'skii, A.M. 1889. Ostrov Sakhalin i ego fauna pozvonochnykh zhivotnykh (Sakhalin Island and its vertebrate fauna). *Zap. Ak. Nauk.*, vol. 60, Appendix no. 5. St. Petersburg.

Nikul'tsev, A.P. and G.A. Predtechenskii. 1957. O lose, kosule i kabane v raione Voronezhskogo zapovednika (Elk, roe deer, and wild boar in Voronezh preserve region). *Tr. Voronezshk. Gos. Zapovedn.*, no. 7. Voronezh.

Noak, T. 1902. Centralasiatische Steinbocke. *Zool. Anz.*, vol. 25.

Nordmann, A. 1838. Über das Vorkommen des Auerochsen in Caucasus. *Bull. Scient. publie par l'Acad. des Sc. de St.-Ptb.*, vol. 3, no. 20. St. Petersburg.

Novikov, B.G. 1957. Nekotorye dannye o faktorakh, vliyayushchikh na razmnozhenie ondatry v del'te Amu-Dar'i (Some data on factors influencing the reproduction of muskrat in Amu-Darya delta). *Zool. Zhurn.*, vol. 36, no. 12.

Novikov, G.A. 1937. Promyslovo-okhotnich'ya fauna severo-zapadnogo Zabaikal'ya (Game fauna of northwest Trans-Baikal). Sb. *Buryat-Mongoliya* (*Tr. SOPS Ser. Vostochno-Sibirsk.*, no. 4). Moscow-Leningrad.

Ogneff, S.I. [Ognev, S.I.] and W.[V.] G. Heptner. 1928. Einige Mitteilungen über die Säugetiere des Mittleren Kopet-Dag under der anliegenden Ebene. *Zool. Anz.*, vol. 75.

Ognev, S.I. 1926. Mlekopitayushchie severo-vostochnoi Sibiri (Mammals of Northeast Siberia). Vladivostok.

Ognev, S.I. 1931. Sobol (Sable). *Tr. po Lesn. Opytn. Delu Tsentr. Lesn. Opytn. Stants.*, no. 14.

Ognev, S.I. 1940. Mlekopitayushchie Tsentral'nogo Tyan'-Shanya (Mammals of central Tien Shan). *Mater. k Pozn. Fauny i Flory SSSR, Nov. Ser., Otd. Zool.*, no. 3.

Ognev, S.I. 1947. Novye dannye po faune mlekopitayushchikh Moskovskoi oblasti (Recent data on the mammalian fauna of Moscow district). Sb. *Ocherki Prirody Podmoskov'ya i Mosk. Obl.* Moscow.

Ognev, S.I. and K.A. Vorob'ev. 1924. Fauna nazemnykh pozvonochnykh Voronezhskoi gubernii (Land Vertebrate Fauna of Voronezh Province). Moscow.

Ognev, S.I. and V.G. Heptner. 1929. Mlekopitayushchie srednego Kopet-Daga i prilezhashchei ravniny (Mammals of central Kopet-

Dag and adjacent plains). *Tr. N.-I. In-ta Zoologii MGU,* vol. 3, no. 1.

Oken's. 1821. *Lehrbuch der Naturgeschichte.* Leipzig.

Okhotina, M.V. 1957. Naledi i ikh znachenie v zhizni nekotorykh zverei (Ice crusts and their importance in the life of some animals). *Uch. Zap. Dal'nevost. Un-ta,* no. 1. Vladivostok.

Olivkov, B.M. and O.A. Nosova. 1940. Nekrobatsillez u parnokopytnykh i kenguru Moskovskogo zooparka (Necrobacillosis in artiodactyls and kangaroos of Moscow Zoological Park). *Tr. Mosk. Zooparka,* vol. 1.

Oloff, H.B. 1951. *Zur Biologie und Okologie des Wildschweines. Beiträge zur Tierkunde und Zierzucht.* Frankfurt-am-Main, vol. 2.

Ostroumov, N.A. 1949. Zhivotnyi mir Komi ASSR. Pozvonochnye (Animals World of Komi Autonomous Soviet Socialist Republic. Vertebrates). Syktyvkar.

Paas, K. 1915. Kratkii obzor pushnogo dela v Rossii (Brief review of the fur industry in Russia). Sb. *Mater. po Voprosam Pushnogo Dela, Izdavaemye P.K. Klepikovym,* no. 1. Moscow.

Pakhtusov, G. 1842. Dnevnye zapiski, vedennye podporuchikom Pakhtusovym pri opisi vostochnogo berega Novoi Zemli, v 1832–1833 gg. (Diary of Second Lieutenant Pakhtusov describing the east coast of Novaya Zemlya in 1832 and 1833). *Zap. Gidrograf. Departam. Morsk. Min-va,* pt. 1. St. Petersburg.

Pallas, P.S. 1771, 1773, and 1776. *Reise durch verschiedene Provinzen des Russischen Reiches.* St. Petersburg, pt. 1, 1771; pt. 2, 1773; pt. 3, 1776.

Pallas, P.S. 1773, 1786, and 1788. Puteshestvie po raznym provintsiyam Rossiiskoi Imperii (Travels in Various Provinces of the Russian State). St. Petersburg, pt. 1, 1773; pt. 2, 1786; pt. 3, 1788.

Pallas, P.S. 1811. *Zoographia Rosso-Asiatica sistens omnium animalium in extenso Imperio Rossico et adjacentibus maribus observatorum. . .* Petropoli.

Palmer, L.J. 1927. Progress of reindeer grazing investigation in Alaska. *US Department of Agriculture,* Bull. no. 1423. Washington.

Palmer, L.J. 1934. Raising reindeer in Alaska. *US Department of Agriculture, Miscellaneous Publications,* no. 207. Washington.

Palmer, L.J. 1944. Food requirements of some Alaskan game animals. *J. Mammal.,* vol. 25, no. 1.

Pashkov, V. 1958. Losi v nizov'yakh r. Urala (Elk in the lower reaches of Ural River). *Okhota i Okhot. Khoz.,* no. 5.

Pasternak, F.A. 1955. Materialy k sistematike i biologii kosuli (Data on the systematics and biology of roe deer). *Uch. Zap. Mosk. Gor.*

Ped. In-ta im. V.P. Potemkina, Kaf. Zool., vol. 38, no. 3.

Pavlov, E.I. 1948. Ptitsy i zveri Chitinskoi oblasti (Birds and animals of Chita district). Chita.

Pavlov, E.I. 1949. Promyslovye zveri Chitinskoi oblasti (Game animals of Chita district). Chita.

Pavlov, N.V. 1931. Kompleksnye stepi i pustyni Karsakpaya (Complex steppes and deserts of Karsakpai). *Pochv. In-t. NKZ Kazakhsk. ASSR*. Moscow.

Pechalin. 1928. Dikie oleni (Wild deer). *Ural'skii Okhotnik*, no. 6.

Peterson, R.L. 1955. *North American Moose*. Toronto.

Petri, B.E. 1927. Olenevodstvo u karagas (Reindeer husbandry in Karagas). *Izv. Biol.-Geograf. N.-I. In-ta Pri Gos. Irkutsk. Un-ta*, vol. 3, no. 2.

Petri, B.E. 1930. Okhota i olenevodst vo u tuturskikh tungusov v svyazi s organizatsiei okhot-khozyaistva (Hunting and reindeer husbandry in Tutur Tungus in view of the organization of game hunting). *Izv. Biol.-Geograf. N.-I. In-ta Pri Gos. Irkutsk. Un-ta*, vol. 5, no. 2.

Pevtsov, M.V. 1883. Ocherk puteshestviya po Mongolii i severnym provintsiyam Vnutrennego Kitaya (Outline of travels in Mongolia and northern provinces of interior China). *Zap. Zap.-Sibirsk. Otd. Russk. Geograf. Ob-va*, vol. 5. Om'sk.

Pfizenmayer, E.W. 1914 (1915). Neskol'ko interesnykh ublyudkov semeistva polorogikh iz Zakavkaz'ya (Some interesting hybrids of cavicorns in Trans-Caucasus). *Izv. Kavkazsk. Muzeya*, vol. 8, nos. 3–4. Tiflis.

Pfizenmayer, E.W. 1929. Biologische und morphologische Notizen über den Kaukasuswisent. *Abhandl. D. Math.-Naturwiss. Abt. d. Bayer. Ak. d. Wiss. (Munchen), Suppl.*, vol. 2.

Pidoplichko, I.G. 1951. O lednikovom periode (The Glacial Period) Kiev, vol. 2.

Pidoplichko, I.G. and V.A. Topachevskii. 1953. Los' i severnyi olen' v doistori-cheskom proshlom (Elk and reindeer in the prehistoric period). *Priroda*, no. 7.

Pinegin, N.V. 1932. Materialy dlya ekonomicheskogo obsledovaniya Novosibirskikh ostrovov (Data on the economic survey of Novosibirsk Island). Polyarn. geofiz. stants. na B. Lyakhovskom, pt. 1 (*Tr. SOPS, Ser. Yakutsk.*, no. 7).

Plechev, E.I. 1939. Promyslovye zveri yugo-vostochnoi Kamchatki (Game animals of southeast Kamchatka). *Izv. Gos. Geograf. Ob-va*, vol. 71, no. 9.

Pleske, F.D. 1887. Kriticheskii obzor mlekopitayushchikh i ptits Kol'skogo poluostrova (Critical Review of Mammals and Birds of Kola Peninsula). St. Petersburg.

Pliginskii, V.G. 1929. Fauna zapadnoi chasti TsChO (Fauna of central chernozem region). *Izv. Kursk. Ob-va Kraevedov,* nos. 1/2. Kur'sk.

Podarevskii, V.B. 1936. Problemy okhotokhozyaistvennoi akklimatizatsii v Vostochnoi Sibiri (Problems of Acclimatizing Game Animals in Eastern Siberia). Irkutsk.

Podsosov, L. 1934. Nekotorye dannye k razmnozheniyu losya v nevole (Some data on the reproduction of elk in captivity). *Byull. Zooparkov i Zoosadov,* nos. 6–7. Moscow.

Podsosov, L.A. 1935. K voprosu razmnozheniya losya v nevole (Reproduction of elk in captivity). *Byull. Zooparkov i Zoosadov,* nos. 10–11. Moscow.

Pod"yapol'skii, G.N. 1950. Zveri, ptitsy Kabardinskoi ASSR i problemy ikh okhrany (Animals and birds of Kabardin Autonomous Soviet Socialist Republic and the problems of their conservation). *Okhrana Prirody,* vol. 11.

Pokhozyaistvennaya perepis' Pripolyarnogo Severa SSSR 1926/27 g. Territorial'nye i grupoovye itogi pokho-zyaistvennoi perepisi (Economic Census of the Polar North of the USSR for 1926 to 1927. Territorial and Groupwise Results of Economic Census).

Pokrovskii, V.S. 1950. Kaban i ondatra v del'te r. Amu-Dar'i (Wild boar and muskrat in Amu-Darya River delta). *Priroda,* no. 7.

Polferov, Ya.Ya. 1896. Okhota v turgaiskoi oblasti (Hunting in Turgai district). Orenburg.

Polikevich, P. 1923. Kratkii ocherk okhoty v Minusinskom uezde i Uryankhaiskom krae (Brief description of hunting in Minusinsk and Uryankhaisk territory). *Okhotnich'e Delo,* nos. 8–9.

Polyakov, G.I. 1914. Poezdka na oz. Zaisan-Nor i Marka-Kul' (Travels on Lake Zaisan-Nor and Marka-Kul'). Moscow.

Polyakov, I. 1873. Geograficheskoe rasprostranenie zhivotnykh v yugo-vostochnoi chasti Lenskogo basseina (Geographic distribution of animals in southeast parts of Lena basin). *Zap. Russk. Geograf. Ob-va,* vol. 3.

Polyakov, I.S. 1873. Etnograficheskie nablyudeniya vo vremya poezdki na yugo-vostok Olonetskoi gubernii (Ethnological observations during travels in southeast Olonets province). *Zap. Russk. Geograf. Ob-va po Otd. Etnografii,* vol. 3.

Polyakov, I.S. 1881. Loshad' Przheval'skogo (Przewalski's horse). *Izv. Russk. Geograf. Ob-va,* vol. 17, no. 1.

Popov, L.N. 1939. Promyslovye mlekopitayushchie vostochnogo poberezh'ya Taimyrskogo poluostrova (Game mammals on the east coast of Taimyr Peninsula). *Tr. N.-I. In-ta Polyarn. Zemledeliya, Ser. Promysl. Khozyaistvo,* no. 8.

Popov, S.P. 1939. Priruchenie i ispol'zovanie losya dlya transporta (Domestication and utilization of elk as a beast of burden). (Sb. *Novoe v Ispol'zovanii Severnogo Olenya i Losya Dlya Transporta*). *Tr. N.-I. In-ta Polyarn. Zemledeliya, Ser. Olenevodstvo,* no. 6.

Popov, V.A. and A.V. Lukin. 1950. Zhivotnyi mir Tatarii (pozvonochnye) [Animal World of Tatary (vertebrates)]. Kazan'.

Popov, V.A., Yu.K. Popov, G.P. Priezzhaev, T.M. Kulaeva, N.I. Voronov, V.I. Garanin, I.V. Nazarova, T.E. Izotova, and L.A. Krasovskaya. 1954. Rezul'taty izucheniya zhivotnogo mira zony zatopleniya Kuibyshevskoi GEC (Results of a study of the animal world in the submergence zone of Kuibyshev hydroelectric power plant). *Tr. Kazansk. Fil. AN SSSR, Ser. Biol. Nauk,* no. 3.

Portenko, L.A. 1941. Fauna Anadyrskogo kraya. Ch. 3. Mlekopitayushchie (Fauna of Anadyr region. Pt. 3. Mammals). *Tr. N.-I. In-ta Polyarn. Zemledeliya, Ser. Promysl. Khozyaistvo,* no. 14.

Potanin, G.N. 1867. Puteshestvie na oz. Zaisan i v rechnuyu oblast' Chernogo Irtysha do oz. Markha-Kul' i gory Sarytau letom 1863 g. (Travels on Lake Zaisan and in the river region of Chernyi Irtysh to Lake Marka-Kul' and Sary-Tau mountains in the summer of 1863). *Zap. Russk. Geograf. Ob-va po Obshch. Geografii,* vol. 1.

Prater, S.H. 1947. *Book of Indian Mammals.* Bombay.

Pretwicz, B. 1886. I jego apologia na seime 1550. *Spisal J. M. Z. Bibliotheca Warczawska 1886,* vol. 3, no. 7.

Przewalski, N.M. 1870. Puteshestvie v Ussuriiskom krae 1867–1869 (Travels in Ussuri territory from 1867 to 1869). St. Petersburg.

Przewalski, N.M. 1883. Iz Zaisana cherez Khami v Tibet i verkhov'va Zheltoi reki (From Zaisan through Khami into Tibet and the Upper Courses of Yellow River). St. Petersburg.

Ptushenko, E.S. 1937. Materialy k poznaniyu teriologicheskoi fauny Kurskogo kraya (Study of theriofauna of Kur'sk territory). Sb. *Pamyati Ak. M.A. Menzbira.* Moscow.

Puzanov, I.I. 1949. Svoeobrazie fauny Kryma i ee proiskhozhdenie (Typical fauna of Crimea and its origin). *Uch. Zap. Gor'kovsk. Un-ta,* no. 14.

Puzanov, I.I., V.I. Kozlov and Ch.P. Kiparisov. 1955. Zhivotnyi mir Gor'kovskoi oblasti (Animal World of Gorkii District). Gorkii.

Radde, G. 1861. Berichte über Reisen im Süden von Ost-Sibirien. *Beiträge zur kenntn. d. Russ. Reiches.* St. Petersburg, vol. 23.

Radde, G. 1862. *Säugethierfauna. Reisen im Süden von Ost-Sibirien.* St. Petersburg, vol. 1.

Radde, G. 1866. Puteshestvie v mingrel'skikh Al'pakh (Travels in Mingrel'sk Alps). *Zap. Kavkazsk. Otd. Russk. Geograf. Ob-va,* vol. 7. Tiflis.

Radde, G. 1886. *Reise an der Persisch-Russischen Grenze.* Leipzig.

Radde, G. 1899. Kolletsii Kavkazskogo muzeya. T. 1. Zool. (Collection of Caucasian Museum, vol. 1, Zoology). Tiflis.

Raesfeld, F. 1956. Das Rehwild. *Naturgeschichte, Hege und Jagd.* Hamburg.

Rak, A.S. 1956. Saigaki v Groznenskoi oblasti (Saiga in Groznyi district). *Izv. Groznensk. Obl. Kraev. Muzeya,* nos. 7–8.

Rakov, N.V. 1949. Los' v Severnom i Zapadnom Kazakhstane (Elk in northern and western Kazakhstan). *Okhrana Prirody,* vol. 7.

Rakov, N.V. 1955. O roli volka i drugikh khishchnikov v ogranichenii chislennosti saigaka (Role of wolf and other predators in limiting saiga population). *Tr. In-ta Zool. AN Kazakhsk. SSR,* vol. 4.

Rakov, N.V. 1956. Nekotorye osobennosti uslovii sushchestvovaniya kabana na Sikhote-Alin (Some characteristics of living conditions of wild boar in Sikhote-Alin). *Byull. Mosk. Ob-va Ispyt. Prirody, Otd. Biol.,* vol. 61, no. 1.

Rakov, N.V. 1956. Saigak v Zapadnom Kazakhstane (Saiga in west Kazakhstan). *Tr. In-ta Zool. AN Kazakhsk. SSR,* vol. 6.

Rakov, N.V. 1957. Opyt aerovizual'nogo ucheta krupnykh mlekopitayushchikh v Tsentral'nom Kazakhstane (Aerovisual count of large mammals in central Kazakhstan). *Zool. Zhurn.,* vol. 36, no. 9.

Rapoport, O. 1958. Losi rasshiryayut svoi areal (Elk extend their geographic range). *Okhota i Okhot. Khoz.,* no. 10.

Rashid-Ad-Din, F. 1952 and 1957. Dzhami-at-tavarik (sbornik letopisei). Baku, vol. 1, 1952; vol. 2, 1957.

Ratzeburg, J. 1856. *Die Wildverderber und ihre Feinde.* Berlin.

Rausch, R. 1953. On the status of some Arctic mammals. *Arctic,* vol. 6, no. 2.

Razevig, V.A. 1904. Kavkazskie gornye kozly (tury) [Caucasian mountain goats (turs)]. *Psovaya i Ruzheinaya Okhota; Ezhemes. Knizhn. Prilozh. k Zhurn.,* vols. 4–6.

Razevig, V.A. 1905. Kavkazskaya serna (Caucasian chamois). *Psovaya i Ruzheinaya Okhota; Ezhemes. Knizhn. Prilozh. k Zhurn.,* vols. 10 and 11/12.

Razevig, V.A. 1909. Kozulya ferganskaya *Capreolus pygargus* var.? (Ferghana roe deer *Capreolus pygargus* var.?). *Sem'ya Okhotnikov,* no. 8.

Razorenova, A.P. 1939. Nekotorye dannye o rasprostranenii mlekopitayushchikh na Altae (Some data on the distribution of mammals in Altai). *Sb. Trud. Zool. Muzeya Pri MGU,* no. 5.

Rebrov, A.F. 1849. Perekochevka antilop, dikikh koz i loshadei v Kumskie kamyshi (Migrations of antelope, wild goat, and horse in Kuma reeds). *Sel'sk. Khoz. i Ovtsevodstvo,* no. 1.

Reynolds, S. 1939. *Monograph* [*of*] *British Pleistocene Mammals.* London, vol. 3, pt. 6.

Rikhter, G.B. 1948. Rol' snezhnogo protsessa v fizikogeograficheskom protsesse (Role of snow processes in the physiogeographic process). *Tr. In-ta Geograf.,* no. 40.

Ritcey, R. and R.J. Edwards. 1958. Parasites and diseases of the Wells Gray moose herd. *J. Mammal.* vol. 39, no. 1.

Rode, P. 1943 and 1944. Mammifères ongulés de l'Afrique Noire. Paris, pt. 1, 1943; pt. 2, 1944.

Romanov, A.A. 1941. Pushnye zveri Lensko-Khatangskogo kraya i ikh promysel (Fur-bearing animals of Lena-Khatanga territory and their hunting). *Tr. N.-I. In-ta Polyarn. Zemledeliya, Ser. Promysl. Khozhaistvo,* no. 17.

Rossikov, K.N. 1890. V gorakh severo-zapadnogo Kavkaza (In the mountains of northwest Caucasus). *Izv. Russk. Geograf. Ob-va,* vol. 26, no. 4.

Rozanov, M.P. 1931. Opyt pereseleniya belovezhskogo zubra v gory Kryma (Resettlement of Belovezh wisent in Crimean mountains). Sb. *Rabot po Izuch. Fauny Krymsk. Gos. Zapovedn.* Moscow.

Rozanov, M.P. 1935. Marshrut zoologicheskogo otryad TKE 1932 g. Obshchii ocherk Pamira. Mlekopitayushchie Pamira (Route of the Zoological Party of Tajikistan Complex Expedition in 1932). Sb. *Materialy po Mlekopitayushchim i Ptitsam Pamira* (*AN SSSR. Tadzhiksk. Kompl. Eksped.,* 1932, no. 32). Leningrad.

Rozanov, M.P. 1937. Zhivotnye oazisov i pustyn' (Animals of oases and deserts). Sb. *Ekspeditsii AN SSSR, 1935.* Moscow-Leningrad.

Rukhlyadev, D.P. 1939. Enzooticheskoe invazionnoe zabolevanie glaz u zubrobizonov (Enzootic infection of eyes in wisent). *Nauch.-Metod. Zap. Komiteta po Zapovedn.,* no. 4.

Rukhlyadev, D.P. 1939. K epizootologii sluchaev sibirskoi yazvy u dikikh kopytnykh zhivotnykh Krymskogo zapovednika (Epizootic incidence of Siberian ulcers in wild ungulates of Crimean preserve). *Nauchn.-Metod. Zap. Gl. Upr. po Zapovedn.,* no. 4.

Rukhlyadev, D.P. 1941. Parazitofauna, zabolevaniya i prichiny otkhoda dikikh mlekopitayushchikh zhivotnykh Krymskogo zapovednika (Parasite fauna, diseases, and factors endangering wild mammals of Crimean preserve). *Nauch.-Metod. Zap. Gl. Upr. po Zapovedn.,* no. 8.

Rukhlyadev, D.P. 1948. Parazity i parazitozy dikikh kopytnykh i khishchnykh zhivotnykh gorno-lesnogo Kryma (Parasites and parasitic diseases in wild ungulates and predators of Crimean montane forest). Sb. *Parazitofauna i Zabolevaniya Dikikh Zhivotnykh.* Moscow.

Rukhlyadev, D.P. 1952. K izucheniyu gel'mintofauny dikogo kabana (Study of helminth fauna of wild boar). *Tr. Gel'mintolog. Labor. AN SSSR,* vol. 6.

Rukhlyadev, D.P. 1959. Gel'mintofauna sern, turov, olenei i kosul' v Kavkazskom zapovednike (Helminth fauna of chamois, tur, deer, and roe deer in Caucasian preserve). *Tr. Kavkazsk. Gos. Zapovedn.,* no. 5. Maikop.

Rukovskii, N.N. 1947. Vliyanie razlivov r. Urala na faunu Gur'evskoi oblasti (Effect of floods in Ural River on fauna of Gur'ev district). *Priroda,* no. 6.

Rul'e, K.F. 1845. O zhivotnykh moskovskoi gubernii ili o glavnykh peremenakh v zhivotnykh pervozdannykh istoricheskikh i nyne zhivushchikh v Moskovskoi gubernii zamechaemykh (Animals of Moscow Province or Major Changes in Extinct and Extant Animals in Moscow Province). Moscow.

Rumyantsev, B.F., N.S. Butarin and V.F. Denisov. 1935. Opyt gibridizatsii kyrdyuchnykh ovets s dikim baranom Tyan'-Shanya (*Ovis poloii karelini* Se.) [Hybridization experiments with Kurdyuk sheep and wild Tien-Shan sheep (*Ovis poloii karelini* Se.)]. Sb. *Vidovaya Gibridizatsiya Domashnikh Zhivotnykh s Dikimi Vidami* (*Tr. Kirgizsk. Kompl. Eksped. 1933–1934* gg., vol. 4, no. 3). Moscow-Leningrad.

Rumyantsev, V.V. 1936. O proiskhozhdenii domashnei loshadi (Origin of domestic horses). *Izv. AN SSSR, Otd. Mat. i Est. Nauk.* Moscow-Leningrad.

Rutilevskii, G.L. 1939. Promyslovye mlekopitayushchie poluostrova Chelyuskina i proliva Vil'kitskogo (Game mammals of Chelyuskin Peninsula and Vil'kits Bay). *Tr. N.-I. In-ta Polyarn. Zemledeliya, Ser. Promysl. Khozyaistvo,* no. 8.

Ruzskii, M. 1898. Zubr, kak vymirayushchii predstavitel' nashei fauny (Wisent as a vanishing representative of our fauna). *Uch. Zap. Kazansk. Veterin. In-ta,* vol. 15, nos. 5–6.

Ryabova, T.I. and A.P. Saverkin. 1937. Dikorastushchie kormovye rasteniya pyatnistogo olenya (Wild food plants of sika). *Tr. Dal'nevost. Fil. AN SSSR, Ser. Botan.,* vol. 2. Vladivostok.

Rychkov, P. 1762. Topografiya Orenburgskaya, i.e., obstoyatel'noe opisanie Orenburgskoi gubernii (Topography of Orenburg, i.e., an Exhaustive Description of Orenburg Province). St. Petersburg.

Rykovskii, A.S. 1957. Gel'mintofauna losya i opyt ee ekologicheskogo analiza (Helminth fauna of elk and its ecological analysis). Kand. Diss.

Rzaczynski, G. 1742. *Annotarium Historiae Naturalis Curiosa Regni Poloniae 1721–1742.*

Sabaneev, L.P. 1868. Materialy dlya fauny Yaroslavskoi gubernii (Data on fauna of Yaroslav province). *Tr. Yaroslavsk. Gub. Statist. Komit.,* no. 4.

Sabaneev, L.P. 1872. Katalog zverei, ptits, gadov i ryb Srednego Urala (Catalog of Animals, Birds, Reptiles, and Fish of Central Urals). Moscow.

Sabaneev, L.P. 1872. Zverinyi promysel v Ural'skikh gorakh (Animal hunting in Ural mountains). *Beseda,* vol. 7.

Sabaneev, L.P. 1875. Kosulya i kozlinyi promysel v Ural'skikh gorakh (Roe deer and goat hunting in Ural mountains). *Priroda,* 3rd year, vol. 4.

Sablina, T.B. 1955. Kopytnye Belovezhskoi Pushchi (Ungulates of Belovezh Forest). *Tr. In-ta Morfol. Zhivotnykh AN SSSR,* no. 15.

Sablinskii, A.K. 1914. Opyt ucheta, sostoyaniya i sostava losinykh stad v Tsarskosel'skom uezde C.-Peterburgskoi gubernii (Census, survival conditions, and herd composition of elk in Tsarskosel'sk district of St. Petersburg province). *Mater. k poznan. Russk. Okhotn. Dela,* no. 3. St. Petersburg.

Safarov, M.A. 1958. Morfologicheskie osobennosti dikogo kabana Azerbaidzhana (ekster'er i inter'er) [Morphological features (external and internal) of wild boar in Azerbaidzhan]. *Izv. AN Azerbaidzhansk. SSR, Ser. Biol. i S.-Kh. Nauk,* no. 3.

Sainio, P. 1956. Hirvikantamme suuruus. *Suomen Riista,* no. 10. Helsinki.

Salesski, P. 1934. Die Verbreitung der Paarhufer in Westsibirien. *Karakulevodstvo i Zverovodstvo,* no. 5.

Salganskii, A.A. 1952. Opyt vypasnogo soderzhaniya pyatnistogo olenya bez izgorodei (Raising sika under free-grazing conditions). *Karakulevodstvo i Zverovodstvo,* no. 5.

Salikhbaev, Kh.S. 1939. Okhotnich'i i promyslovye zveri i ptitsy Guzarskogo raiona (Game animals and birds of Guzar region). *Tr. Uzbeksk. Zool. Sada,* vol. 1. Tashkent.

Salikhbaev, Kh.S. 1950. Okhotnich'e-promyslovye zhivotnye del'ty Amu-Dar'i (Kara-Kalpakiya) i mery ikh ratsional'nogo ispol'zovaniya [Game animals of Amu-Darya delta (Kara-Kalpakiya) and measures for their rational utilization]. Sb. *Mater. po Proizvodit. Silam Uzbekistana,* no. 1. Tashkent.

Samorodov, A.V. 1939. K faune mlekopitayushchikh zemli olyutorskikh koryakov (Mammalian fauna of Olyutorsk Koryaks). *Sb. Trud. Gos. Zool. Muzeya Pri MGU,* vol. 5.

Sapozhnikov, V.V. 1911. Mongol'skii Altai (Mongolian Altai). Tom'sk.

Sarkisov, A.A. 1944. Armeniiskii muflon Nasonova *Ovis ophion armeniana* Nas. [Armenian mouflon (*Ovis ophion armeniana* Nas.)]. *Tr. Erevansk. Zool. Parka AN Armyansk. SSR,* no. 3.

Sarkisov, A.A. 1944. Kavkazskaya serna (*Rupicapra rupicapra caucasica* Lyd.) v Armenii [Caucasian chamois (*Rupicapra rupicapra caucasica* Lyd.) in Armenia]. *Tr. Erevansk. Zool. Parka AN Armyansk. SSR,* nos. 1–2.

Sarkisov, A.A. 1944. O migratsiyakh *Ovis ophion armeniana* Nas. (Migrations of *Ovis ophion armeniana* Nas.). *Tr. Erevansk. Zool. Parka AN Armyansk. SSR,* nos. 1–2.

Sarkisov, A.A. 1946. O rasprostranenii onagra (*Equus hemionus*) v priaraksinskikh stepyakh Armenii [Distribution of onager (*Equus hemionus*) in pri-Araksin steppes of Armenia]. *Izv. AN Armyansk. SSR,* no. 3.

Sarkisov, A.A. 1954. Geneticheskie svyazi vidov i ikh arealy rasprostraneniya (Genetic relations of species and their distribution). *Tr. Erevansk. Zooparka,* no. 4.

Sarychev, G. 1802. Puteshestvie flota kapitana Sarycheva po Severo-Vostochnoi chasti Sibiri, Ledovitomu moryu i Vostochnomu okeanu, Ch. 1–2 (Journey of Captain Sarychev's Fleet along Northeastern Parts of Siberia, Arctic Ocean, and East Sea. Pts. 1–2). St. Petersburg.

Satunin, K.A. 1895. Pozvonochnye Moskovskoi gubernii. Vyn. 1. Mlekopitayushchie (Vertebrates of Moscow province. No. 1. Mammals). *Izv. Ob-va Lyubit. Est. Antrop. i Etnografii,* vol. 36; *Tr. Zoolog. Otd.,* vol. 10.

Satunin, K. 1896. Vorläufige Mitteilungen über die Säugetierfauna der Kaukasusländer. *Zool. Lahrb. Syst.,* vol. 9.

Satunin, K.A. 1898. Kavkazskii zubr (Caucasian wisent). *Estestvoznanie i Geografiya,* no. 2.

Satunin, K.A. 1906. Ein neues Reh vom Tien-Shan. *Zool. Anz.,* vol. 30, nos. 17/18.

Satunin, K.A. 1906. Mlekopitayushchie Talysha i Muganskoi stepei (Talysh and Mugansk steppe mammals). *Izv.Kavkazsk. Muzeya,* vol. 2. Tiflis.

Satunin, K.A. 1908. Zametka o dzheirane (Notes on goitered gazelle). *Okhotnichii Vestnik,* no. 1.

Satunin, K.A. 1914. Kavkazskii zubr (Caucasian wisent). *Ocherki Rodinovedeniya Kavkaza,* no. 4, Tiflis.

Savinov, V.A. and A.N. Lobanov. 1958. Zveri Vologodskoi oblasti (Animals of Vologda District). Vologda.

Schrenk, L.V. 1859. *Säugetiere des Amurlandes. Reisen und Forschungen im Amur-Lande.* St. Petersburg, vol. 1.

Schwarz, E. 1935. On ibex and wild goat. *Ann. Mag. Nat. Hist.,* 10th ser., vol. 16.

Sdobnikov, V.M. 1935. K voprosu o sostave osennego korma severnykh olenei (Composition of autumn food of reindeer). *Tr. Arktichesk. In-ta,* vol. 24.

Sdobnikov, V.M. 1935. Materialy po voprosu o zimnem pitanii severnogo olenya (Data on winter food of reindeer). *Tr. Arktichesk. In-ta,* vol. 24.

Sdobnikov, V.M. 1935. Vzaimootnosheniya severnogo olenya s zhivotnykh mirom tundry i lesa (Interrelations of reindeer with animals of the tundra and forest). *Tr. Arktichesk. In-ta,* vol. 24.

Sdobnikov, V.M. 1939. K voprosu ob ekologii severnogo olenya (Ecology of reindeer). Sb. *Voprosy Ekologii i Biotsenol.,* nos. 5–6.

Sdobnikov, V.M. 1958. Dikii olen' Taimyra i uporyadochenie ego promysla (Wild deer of Taimyr and regulation of its hunting). Sb. *Probl. Severa,* no. 2. Moscow.

Sedel'nikov, A.P. and N.A. Borodin. 1903. Rastitel'nyi i zhivotnyi mir (Plant and animal world). *Rossiya, Kirgizsk. Krai,* vol. 18.

Selevin, V.A. 1924. Uvelichenie dikikh baranov v Del'begeteiskikh gorakh (Increase in wild sheep in population in Del'begeteisk mountains). *Okhotnik Altaya,* nos. 1–3.

Selevin, V.A. 1925. O redkikh okhotnich'ikh zveryakh Del'begeteiskikh gor (Rare game animals of Del'begeteisk mountains). *Okhotnik,* nos. 6–7.

Selevin, V.A. 1928. Ob okhotnich'ei fauna Semipalatanskogo uezda (Game fauna of Semipalatinsk district). *Okhotnik,* no. 5.

Selevin, V.A. 1932. K istorii ischeznoveniya kulana iz severovostochnogo Kazakhstana (History of the disappearance of kulan from northeast Kazakhstan). *Okhotnik i Rybak Sibiri,* no. 4.

Selevin, V.A. 1937. Perechen' mlekopitayushchikh okrestnostei Semipalatinska (List of mammals around Semipalatinsk). *Byull. Sr.-Az. Gos. Un-ta,* nos. 22 and 36.

Selevin, V.A. 1938. Poslednie kulany Semipalatinskogo Priirtysh'ya (Last of the kulans of Semipalatinsk-Pri Irtysh). *Byull. Sr.-Az. Gos. Un-ta,* nos. 4 and 22.

Semenov, A.B. 1957. Metodika kolichestvennogo ucheta losei po sledam s samoleta (Aerial method for census of elk from their hoofprints). Sb. *Voprosy Ekologii,* vol. 2. Kiev.

Semenov, B.T. 1956. Metodika kolichestvennogo ucheta losei po sledam s samoleta (Aerial method for census of elk from their hoofprints). *Tr. Vses. N.-I. In-ta Okhot. Promysla,* no. 16.

Semenov-Tyan-Shanskii, O.I. 1948. Dikii severnyi olen' na Kol'skom poluostrove (Wild reindeer on Kola Peninsula). *Tr. Laplandsk. Gos. Zapovedn.,* no. 2. Moscow.

Semenov-Tyan-Shanskii, O.I. 1948. Los' na Kol'skom poluostrove (Elk on Kola Peninsula). *Tr. Laplandsk. Gos. Zapovedn.,* no. 2. Moscow.

Semenov-Tyan-Shanskii, O.I. 1952. Kolichestvennyi uchet dikogo severnogo olenya v Laplandskom zapovednike (Census of wild reindeer in Lapland preserve). Sb. *Metody Ucheta Chislennosti i Geograficheskogo Raspredeleniya Nazemnykh Pozvonochnykh.* Moscow.

Serzhanin, I.N. 1955. Mlekopitayushchie Belorusskoi SSR (Mammals of Belorussian Soviet Socialist Republic). Minsk.

Seton, E.T. 1909–1910. *Life Histories of Northern Animals.* London, vol. 1, 1909; vol. 2, 1910.

Severtsov, N.A. 1855. Periodicheskie yavleniya v zhizni zverei, ptits i gadov Voronezhskoi gubernii (Periodic Phenomena in the Life of Animals, Birds, and Reptiles of Voronezh Province). Moscow.

Severtsov, N.A. 1861. Zveri Priural'skogo kraya (Animals of Cis-Ural territory). *Akklimatizatsiya,* vol. 2, no. 2.

Severtsov, N.A. 1873 (1872). Vertikal'noe i gorizontal'noe raspredelenie turkestanskikh zhivotnykh (Vertical and horizontal distribution of Turkestan animals). *Izv. Ob-va Lyubit. Est., Antrop. i Etnogr.,* vol. 8, no. 2.

Severtsov, N.A. 1873. Arkary (gornye barany) [Argali (mountain sheep)]. *Priroda,* vol. 1.

Severtsov, S.A. 1926. Sud'ba zubrov (Fate of wisent). Sb. *Okhotnik,* no. 4.

Severtsov, S.A. 1929. Poezdka v zapovednik Aksu-Dzhebagly (Journey into Aksu-Dzhebaglin Preserve). *Zemlevedenie,* vol. 31, nos. 2–3.

Severtsov, S.A. 1933. O padezhakh dikikh zhivotnykh (Mortality of wild animals). *Sov. Sever.,* no. 5.

Severtsov, S.A. 1940. Belovezhskaya Pushcha (Belovezh Forest). *Priroda,* no. 10.

Severtsov, S.A. 1940. Vidovye konstanty razmnozheniya belovezhskogo zubra i dinamika naseleniya etogo vida (Species constants of reproduction of Belovezh wisent and its population dynamics). *Tr. In-ta Evolyuts. Morfol. im. A.N. Severtsova,* vol. 3, no. 1.

Severtsov, S.A. 1941. Okhotnich'ya fauna Pribaltiki (Game animals of Pri-Baltics). *Sovet. Okhotnik,* no. 1.

Severtsov, S.A. 1941. Dinamika naseleniya i prisposobitel'naya evolyutsiya zhivotnykh (Population Dynamics and Adaptive Evolution of Animals). Moscow-Leningrad.

Severtsov, S.A. and T.B. Sablina. 1953. Olen', kosulya i kaban v zapovednike Belovezhskaya Pushcha (Deer, roe deer, and wild boar in Belovezh Forest preserve). *Tr. In-ta Morfol. Zhivotnykh AN SSSR,* no. 9.

Shaberdin, D.V. 1930. Mlekopitayushchie i ptitsy Srednego Prikam'ya (Mammals and birds of central Kama). *Tr. Nauchn. Ob-va po Izuch. Vyatskogo Kraya,* no. 6. Vyatka.

Shaposhnikov, F.D. 1953. O "solontsevanii" dikikh kopytnykh zhivotnykh v gornotaezhnom Altae (Salt tolerance of wild ungulates in montane taiga of Altai). *Byull. Mosk. Ob-va Ispyt. Prirody. Otd. Biol.,* vol. 58, no. 1.

Shaposhnikov, F.D. 1955. K ekologii i morfologii altaiskogo severnogo olenya (Ecology and morphology of Altai reindeer). *Zool. Zhurn.,* vol. 34, no. 1.

Shaposhnikov, F.D. 1956. Materialy k ekologii kabargi saverovostochnogo Altaya (Data on the ecology of northeastern Altai musk deer). *Zool. Zhurn.,* vol. 35, no. 7.

Shaposhnikov, F.D. 1957. Gornye barany Zapadnogo Tyan'-Shanya (Mountain sheep of western Tien Shan). *Priroda,* no. 1.

Shaposhnikov, L.V. 1951. Pitanie losya v Mordovskom zapovednike i mery k dal'nei-shemu uvelicheniyu ego pogolov'ya (Food for elk in Mordov preserve and measures for increasing its population). *Okhrana Prirody,* vol. 13.

Sharf, F.F. 1918. Evropeiskie zhivotnye (European Animals). Moscow.

Shastin, L.P. 1939. Nazemnye mlekopitayushchie severozapadnoi chasti Taimyr-skogo poluostrova (Land mammals of northwest Taimyr Peninsula). *Tr. N.-I. In-ta Polyarn. Zemledeliya, Ser. Promysl. Khozyaistvo,* no. 8.

Shaternikov, T.M. and N.V. Rumyantsev. 1934. Kulany (Kulans). *Konevodstvo,* nos. 2–3.

Shaw, C.W. et al. 1958. *Report on the Mammals of Northern China.* Peking.

Shchegolev, R.N. 1935. Fauna, biologiya i ekonomicheskoe znachenie mlekopitayushchikh Cherepovetskoi gubernii (Fauna, biology, and economic importance of mammals in Cherepovets province). *Tr. Cherepovets. Ob-va Izuch. Mestnogo Kraya.*

Shchekin, V.A. and A.V. Shkurgin. 1950. Rezul'taty gibridizatsii loshadei i oslov s kulanami (Results of hybridization of horses and asses with kulans). *Tr. Vses. N.-I. In-ta Konevodstva,* vol. 18.

Shcherbakov, A.N. 1953. Kabarga, ee ekologiya i khozyaistvennoe ispol'zovanie (Musk deer, its ecology and economic exploitation). Kand. Diss.

Shereshevskii, E.I. 1931. Muflon (*Ovis musimon* Pall.) v Krymskom zapovednike [Mouflon (*Ovis musimon* Pall.) in Crimean preserve]. Sb. *Rabot po Izucheniyu Fauny Krymsk. Gos. Zapovedn.* Moscow.

Shereshevskii, E.I. and P.A. Petryaev. 1949. Spravochnik okhotnika-polyarnika (Handbook for the Polar Hunter). Moscow-Leningrad.

Shestoperov, E.L. 1936. Materialy k poznaniyu fauny Karlyukskogo raiona TSSR (Study of fauna of Karlyuk region of Turkmenian Soviet Socialist Republic). *Byull. Turkmensk. Zool. Stant.,* no. 1. Ashkhabad.

Shillinger, F.F. 1928. Kaban (Wild Boar). Moscow.

Shil'der, V.A. 1901. Kubanskaya okhota . . . velikogo knyazya Serg. Mikh. v 1898 g. (Kuban hunting of . . . Great Prince Serg. Mich. in 1898). *Priroda i Okhota,* May.

Shiryaev, D.T. and A.T. Shapovalov. 1956. Issledovanie na zarazhennost' brutsellezom saigakov v Severo-Zapadnom Prikaspii (Study of brucellosis infection of saiga in northwest Cis-Caspian). *Tr. Rostovskogo n Donu Gos. N.-I. Protivochumn. In-ta,* vol. 10.

Shitkov, B.M. 1936. Über den Elch in USSR. *Zeitschr. f. Säugetierk,* vol. 11, Berlin.

Shmit, E. 1930. Promysel dikikh olenei (Hunting of wild deer). *Okhotnik,* no. 11.

Shmit, E.V. 1936. Opyt opredeleniya prodolzhitel'nosti beremennosti domashnego severnogo olenya (Determining the gestation period in domestic reindeer). *Sov. Olenevodstvo,* no. 8.

Shnarevich, I.D. 1948. Materialy po biologii gornogo kozla (Data on the biology of mountain goat). *Tr. Alma-Atinsk. Zooparka,* no. 1.

Shnarevich, I.D. 1952. Opyt kolichestvennogo ucheta nekotorykh promyslovykh zhivotnykh Alma-Atinskogo zapovednika (Numerical counting of some game animals in Alma-Ata preserve). Sb. *Metody Ucheta Chislennosti i Geograficheskogo Raspredeleniya Nazemykh Pozvonochnykh.* Moscow.

Shnitnikov, V.N. 1936. Mlekopitayushchie Semirech'ya (Semirech'e Mammals). Moscow-Leningrad.

Shostak, A.S. 1927. Okhotnich'e khozyaistvo Dzhetysu (Game Husbandry of Dzhetysu). Alma-Ata.

Shtegman, B.K. 1949. Promyslovaya fauna del'ty r. Ili. I. Zveri

(Game fauna of Ili River delta. 1. Animals). *Okhrana Prirody,* vol. 8.

Shubin, G.G. and Yu.P. Yazan. 1958. Losepromyslovoe khozyaistvo (Elk hunting). *Okhota i Okhot. Khoz.,* no. 7.

Shubin, G.G. and Yu.P. Yazan. 1959. Opyt organizatsii i vedeniya losepromyslovogo khozyaistva (Organization and administration of elk farming). *Tr. Pechoro-Ilychsk. Gos. Zapovedn.,* no. 7. Syktyvkar.

Shukurov, G.Sh. 1951. Bol'shie Balkhany i okhrana ikh fauny (The Great Balkhans and conservation of their fauna). *Okhrana Prirody,* vol. 13.

Shul'pin, L.M. 1948. Materialy po mlekopitayushchim i gadam Talasskogo Ala-Tau (Data on mammals and reptiles of Talas Alatau). *Izv. AN Kazakhsk. SSR,* no. 51, *Ser. Zool.,* no. 7.

Shul'ts, R.S. and A.N. Kadenatsii. 1950. Gel'minty dal'nevostochnogo gorala(Helminths of Far East goral). *Tr. Gel'mintol. Labor. AN SSSR,* vol. 3.

Shvarts, S.S., V.N. Pavlinin and N.N. Danilov. 1951. Zhivotnyi mir Urala (Animals of the Urals). Sverdlov.

Siebold, Ph. Fr. de. 1847. Fauna Japonica . . . .

Siivonen, L. 1953. Letsakauris leviämässä maahamme. *Suomen Riista,* no. 8.

Silant'ev, A.A. 1898. Obzor promyslovykh okhot v Rossii (Review of Game Hunting in Russia). St. Petersburg.

Simpson, G.G. 1945. The principles of classification and a classification of mammals. *Bull. Am. Mus. Nat. Hist.,* vol. 85. New York.

Skalon, V.N. 1929. Gornyi kozel v Altaisko-Sayanskoi sisteme (Mountain goat in Altai-Sayan system). *Okhrana Prirody,* vol. 3.

Skalon, V.N. 1931. Olenevodstvo v basseine r. Taza (Reindeer farming in Taz River basin). *Sov. Sever.,* nos. 3–4.

Skalon, V.N. 1936. Materialy k poznaniyu fauny yuzhnykh granits Sibiri (Data on fauna of the southern borders of Siberia). *Izv. Gos. Protivochumn. In-ta Sibiri i DVK,* vol. 3. Irkutsk.

Skalon, V.N. 1937. Kozulya i izyubr' v Yuzhnoi Yakutii (Roe deer and Manchurian wapiti in southern Yakutia). *Boets-Okhotnik,* no. 9.

Skalon, V.N. 1940. Dikie oleni Novo-Sibirskikh ostrovov (Wild deer of Novosibirsk Islands). *Priroda,* no. 2.

Skalon, V.N. 1946. O rasshirenii kozulei svoego areala v Sibiri (Enlargement of roe deer geographic range in Siberia). *Priroda,* no. 6.

Skalon, V.N. 1949. O bylom rasprostranenii dikikh baranov i kulana v Yuzhnoi Sibiri (Former distribution of wild sheep and kulan in southern Siberia). *Tr. Kyakhtinsk. Kraeved. Muzeya i Kyakhtinsk. Otd. Vses. Geograf. Ob-va,* vol. 16, no. 1.

Skalon, V.N. 1951. O nekotorykh promyslovykh mlekopitayushchikh Bodaibinskogo raiona Irkutskoi oblasti (Some game mammals of Bodaybo region of Irkutsk district). *Byull. Mosk. Ob-va Ispyt. Prirody, Otd. Biol.,* vol. 56, no. 1.

Skalon, V.N. and P.P. Khoroshikh. 1958. Domashnie losi na naskal'nykh risunkakh Sibiri (Domestic elk in rock drawings in Siberia). *Zool. Zhurn.,* vol. 37, no. 3.

Skalon, V., I. Shcherbakov and M. Bazykin. 1941. Novye materialy po rasprostraneniyu promyslovykh mlekopitayushchikh v Yakutii (Recent data on distribution of game mammals in Yakutia). *Priroda i Sots. Khoz.,* vol. 8, pt. 2.

Skalon, N.N. and M.I. Shikin. 1951. Perspektivy ekspluatatsii losya v Tuvinskoi avtonomnoi oblasti (Prospects of the exploitation of elk in Tuva Autonomous Region). *Okhrana prirody,* vol. 12.

Skorin, I.E. and V. Shubin. 1950. Yashchur u saigakov (Hoof-and-mouth disease among saiga). *Veterinariya,* no. 10.

Skorobogatov, 1924. Turkestanskaya okhota (Hunting in Turkestan). *Turkestansk. Okhotnik,* nos. 1–4.

Skrobov, V.D. 1958. Prodvizhenie zhivotnykh lesnoi zony v tundru (Advancement of forest zone animals into the tundra). *Priroda,* no. 11.

Skrobov, V.D. 1958. Migratsiya losei v tundru (Migration of elks into the tundra). *Okhota i Okhot. Khoz.,* no. 4.

Skuncke, F. 1949. *Älgen. Studier, jakt och vard.* Stockholm.

Sledy okhotnich'ikh zhivotnykh. Priloz. k zhurn. (Tracks of game animals. Appendix to journal). *Okhotnichii Vestn.* Moscow, 1905.

Slovtsov, I.Ya. 1892. Pozvonochnye zhivotnye Tyumen'skogo okruga i ikh rasprostranenie v Tobol'skoi gubernii (Vertebrate animals of Tyumen region and their distribution in Tobol'sk province). *Mater. k Poznan. Fauny i Flory Rossiisk Imperii, Otd. Zool.,* no. 1.

Slovtsov, I.Ya. 1897. Putevye zapiski, vedennye vo vremya poezdki v Kokchetavskii uezd, Akmolinskoi oblasti v 1878 g. (Travel records made during journeys in Kokchetav district, Akmolinsk district in 1878). *Zap. Zap.-Sib. Otd. Russk. Geograf. Ob-va,* vol. 21.

Slovtsov, I.Ya. 1897. Spisok mlekopitayushchikh i ptits, naidennykh mezhdu Omskom, Petropalvlovskom, Akmolinskom i Atbasarom (List of mammals and birds found between Om'sk, Petropavlovsk, Akmolinsk, and Atbasar). *Zap. Zap.-Sib. Otd. Russk. Geograf. Ob-va,* vol. 21.

Sludskii, A.A. 1939. Pushnye zveri Kazakhstana (Fur-bearing animals of Kazakhstan). Alma-Ata.

Sludskii, A.A. 1950. Losi v Kazakhstane i zadachi ikh khozyaistvennogo ispol'zovaniya (Elk in Kazakhstan and problems of their economic utilization). *Izv. AN Kazakhsk. SSR,* no. 84, *Ser. Zool.,* no. 9.

Sludskii, A.A. 1953. Dzhuty v pustnykh Kazakhstana i vliyanie ikh na chislennost' zhivotnykh (Prolonged snow cover in Kazakhstan deserts and their effect on animal populations). *Tr. In-ta zoologii AN Kazakhsk. SSR,* vol. 2.

Sludskii, A.A. 1953. Vyselenie "taezhnykh" zverei v lesostep'e i stepi Zapadnoi Sibiri i Kazakhstana (Settlement of taiga animals in the forest-steppes and steppes of western Siberia and Kazakhstan). *Byull. Mosk. Ob-va Ispyt. Prirody, Otd. Biol.,* vol. 58, no. 2.

Sludskii, A.A. 1953. Otryad khishchnye (Carnivora) (Order Carnivora). In *Zveri Kazakhstana* by A.V. Afanas'ev et al. Alma-Ata.

Sludskii, A.A. 1954. Rol' dikikh mlekopitayushchikh v rasprostranenii infektsionnykh zabolevanii domashnikh zhivotnykh (Role of wild mammals in the spread of infectious diseases among domestic animals). Sb. *Prirodnaya Ochagovost' Zaraznykh Boleznei v Kazakhstane,* no. 2. Alma-Ata.

Sludskii, A.A. 1955. Saigak v Kazakhstane (Saiga in Kazakhstan). *Tr. In-ta Zool. AN Kazakhsk. SSR,* vol. 4.

Sludskii, A.A. 1956. Razmnozhenie dzheirana (Reproduction in goitered gazelle). *Tr. In-ta Zool. Kazakhsk. SSR,* vol. 6.

Sludskii, A.A. 1956. Fauna Kazakhstana i ee okhrana (Fauna of Kazakhstan and its conservation). *Tr. In-ta Zool. AN Kazakhsk. SSR,* vol. 6.

Sludskii, A.A. 1956. Kaban (Morfologiya, ekologiya, khoz. i epizootologicheskoe znachenie, promysel) [Wild Boar (Morphology, Ecology, Economic and Epizootic Significance, and Hunting]. Alma-Ata.

Smirnov, D. 1914. Etyud iz zhizni dzheirana v Zakaspiiskikh stepyakh (Study of the life of goitered gazelle in Trans-Caspian steppes). *Nasha Okhota,* February.

Smirnov, D. 1928. Poval'nye bolezni domashnikh zhivotnykh opasny zveryu (Serious epidemic diseases of domestic animals). *Okhotnik i Pushnik Sibiri,* no. 6.

Snethlage, K. 1949. *Das Schwarzwild,* 2. Aufl. Frankfurt a. Main.

Sokolov, I.I. 1933. K voprosu ob olenevodstve na evropeiskikh ostrovakh Sovetskoi Arktiki (Reindeer husbandry in the European islands of Soviet Arctic). *Arctica,* vol. 1.

Sokolov, I.I. 1935. Materialy k kharakteristike ekster'era i biologii domashnego olenya Bol'shezemel'skoi tundry (External characters and biology of domestic deer of Bol'shezemel'sk tundra). *Tr. Arktichesk. In-ta,* vol. 24.

Sokolov, I.I. 1937. Polovozrastnaya i rasovaya izmenchivost'cherepa dikogo i domashnego severnogo olenya (Sex, age, and racial variability in the skull of wild and domestic reindeer). *Sov. Olenevodstvo,* no. 9.

Sokolov, I.I. 1949. Opyt estestvennoi klassifikatsii semeistva polorogikh (Bovidae) na osnove kraniologicheskikh dannykh (Natural classification of the family Bovidae based on craniological data). Dokt. Diss.

Sokolov, I.I. 1953. Opyt estestvennoi klassifikatsii polorogikh (Bovidae) (Natural classification of Bovidae). *Tr. Zool. In-ta AN SSSR,* vol. 14.

Sokolov, I.I. 1956. K metodike opredeleniya vozrasta kosuli (*Capreolus capreolus* L.) [Method for determining the age of roe deer (*Capreolus capreolus* L.)]. *Zool. Zhurn.,* vol. 35, no. 8.

Sokolov, I.I. 1958. V zapovednike Barsa-Kel'mes (Bars-Kel'mes preserve). *Okhota i Okhot. Khoz.,* no. 9.

Sokolov, S.S. 1939. Materialy k ekologii arkhara *Ovis poloi* i nekotorykh drugikh kopytnykh Alma-Atinskogo gos. zapovednika [Ecology of argali sheep (*Ovis poloi*) and other hoofed animals of Alma-Ata state preserve]. *Zool. Zhurn.,* vol. 18, no. 3.

Sokolov, S.S. 1951. Materialy po ekologii saigi (Data on the ecology of saiga). *Vestn. AN SSSR,* no. 3.

Sokolov, S.S. and N.I. Suvorov. 1955. Migratsii saigi na sezonnye pastbishcha Bet-Pak-Dala (Saiga migrations into seasonal pastures of Bet-Pak-Dala). *Uch. Zap. Alma-Atinsk., Ped. In-ta,* vol. 7.

Sokolova, I.B. 1954. Dikie zhvachnye kak rezervaty gel'mintozov sel'skokhozyaistvennykh zhivotnykh v Kazakhstane (Wild ruminants as vectors of helminthiases of farm animals in Kazakhstan). Sb. *Prirodnaya Ochagovost' Zaraznykh Boleznei v Kazakhstane,* no. 2. Alma-Ata.

Sokolova, I.B. 1954. Gel'mintofauna dikikh zhvachnykh Kazakhstana (Helminth fauna of wild ruminants of Kazakhstan). *Vestn. AN Kazakhsk. SSR,* no. 5.

Sokolova, I.B. and S.N. Boev. 1950. Materialy po gel'mintofaune dikikh zhvachnykh zhivotnykh Kazakhstana (Data on helminth fauna of wild ruminants of Kazakhstan). *Izv. AN Kazakhsk. SSR, Ser. Parazitol.,* no. 8.

Sokol'nikov, N.P. 1927. Okhotnich'i i promyslovye zveri Anadyrskogo krya (Game and hunting animals of Anadyr territory). *Byull. Mosk. Ob-va Ispyt. Prirody. Otd. Biol.*, vol. 36, nos. 1–2.

Sokur, I.T. 1952. Zveri Sovetskikh Karpat i ik khozyaistvennoe ispol'zovanie (Animals of Soviet Carpathians and Their Utilization). Kiev.

Solov'ev, D.K. 1920. Sayanskaya okhotnich'e-promyslovaya ekspeditsiya (Sayan Game Hunting Expedition), Petrograd.

Solov'ev, D.K. (ed.). 1921. Sayanskii promyslovo-okhotnichii raion i sobolinyi promysel v nem (Sayan game hunting region and sable trade in it). *Tr. Eksped. po Izuch. Sobolya i Issled. Sobolinogo Promysla,* ser. II, *Sayanskaya Eksped.*

Solov'ev, D.K. 1922. Promysly kopytnykh zverei i lesnoi dichi v Rossii (Hunting of hoofed animals and wild forest animals of Russia). *Ezhegod. Vseros. Soyuza Okhotnikov.* Moscow.

Soroka, B. 1957. O saigakakh (Saigas). *Okhota i Okhot. Khoz.,* no. 8.

Sowerby, A. de, C. 1923. *The Naturalist in Manchuria.* Tientsin.

Sozont'ev, G. 1925. Okhota i okhotniki v Kazalinskom uezde (Hunting and hunters in Kazalinsk district). *Okhotnik,* no. 2.

Spangenberg. 1918. Bemerkungen über den Raupenfrass im Nadelholz, besonders in den Forsten der Oberlausitz. *Forst- und Jagd. Archiv von und für Preussen. Jahrg.*

Spangenberg, E.P. 1936. Okhotnich'ya fauna Kirgizskogo khrebta (Game fauna of Kirgizian range). *Boets-Okhotnik,* no. 5.

Stanyukovich, K.V. 1950. O roli dikikh kopytnykh v obrazovanii peskov (Role of wild ungulates in the formation of deserts). *Soobshchen. Tadzhiksk. Fil. AN SSSR,* no. 24.

Stepnyak. 1896. Okhota na kulanov (Hunting kulans). *Priroda i Okhota,* no. 3, March.

Stepnyak. 1896. Okhota na saigakov (Hunting saigas). *Okhotnich'ya Gazeta,* no. 4.

Strautman, E.I. 1953. Otryad parnokopytnye (Order Artiodactyla). In *Zveri Kazakhstana* by A.V. Afanas'ev et al., Alma-Ata.

Strautman, E.I. 1953. Otryad neparnokopytnykh (Order Perissodactyla). In *Zveri Kazakhstana* by A.V. Afanas'ev et al., Alma-Ata.

Stroganov, S.U. 1934. Zametki po faune promyslovykh mlekopitayushchikh severovostochnoi chasti Zapadnoi oblasti (Notes on fauna of game mammals of northeastern part of the western region). *Uch. Zap. Mosk. Gos. Un-ta,* no. 2.

Stroganov, S.U. 1934 and 1936. Fauna mlekopitayushchikh Valdaiskoi vozvyshennosti (Mammalian fauna of Valdaisk upland). *Zool. Zhurn.,* vol. 13, no. 4; vol. 15, nos. 1 and 3.

Stroganov, S.U. 1949. Opredelitel' mlekopitayushchikh Karelii (Guide to Mammals of Karelia). Petrozavodsk.

Stroganova, A.S. 1951. Poyavlenie losei v Stalingradskoi oblasti (Appearance of elk in Stalingrad district). *Priroda,* no. 6.

Sultanov, G. 1939. Okhotnich'i i promyslovye zveri i ptitsy Shirabadskogo raiona (Game and hunting animals and birds of Shirabad region). *Tr. Uzbek. Zool. Sada,* vol. 1.

Sultanov, G.S. 1953. Vintorogii kozel v Uzbekistane (Markhor in Uzbekistan). *Tr. In-ta Zool. i Parazitol. AN Uzbeksk. SSR,* vol. 2, Zoologiya.

Sushkin, P.P. 1915. Poezdka v yugo-vostochnyi Altai i severozapadnuyu Mongoliyu i zametki o ptitsakh etoi mestnosti (Journey into southeast Altai and northwest Mongolia and notes on birds of this locality). *Ornitolog. Vestn.*

Suslov, I.M. 1927. Okhota u tungusov (etnograf. ocherk) [Hunting by the Tungus (an ethnographic outline)]. *Okhotnik i pushnik Sibiri,* no. 1.

Svanbaev, S.K. 1958. Fauna koktsidii dikikh kopytnykh zhivotnykh Kazakhstana (Coccidian fauna of wild ungulates of Kazakhstan). *Tr. In-ta Zool. AN Kazakhsk. SSR,* vol. 9, *Parazitol.*

Sysoev, N. 1955. Okhotnich' i bogatstva nashei oblasti (Game Riches of Our Region). Vladimir.

Sytin, V. 1927. O saigake v Volgo-Kumskikh stepyakh (Saiga in Volga-Kuma steppes). *Okhotnik,* no. 2.

Szaflarski, J. 1955. Choroba cieszynske u dzikow, *Mec. Weteryn,* vol. 11, no. 1.

Tarasov, P.P. 1956. O nekotorykh osobennostyakh morfologii severnogo olenya kak zhivotnogo tundry (Some morphological characteristics of reindeer as a tundra animal). *Byull. Mosk. Ob-va Ispyt. Prirody, Otd. Biol.,* vol. 61, no. 4.

Tarasov, V.P. 1935. Tsenuroz u saigi (Cenurosis in saiga). *Priroda,* no, 6.

Tatarinov, K.A. 1956. Zviri zakhidnikh oblastei Ukraini (Animals of Western Districts of the Ukraine). Kiev.

Tate, G.H.H. 1947. *Mammals of Eastern Asia.* New York.

Tatishchev, V.N. 1950. Izbrannye trudy po geografii Rossii (Collected Works on the Geography of Russia). Moscow.

Temmink, C.J. 1847. Apercu général et spécifique sur les mammiferes qui habitent le Japon et les îles qui en dependent. *Fauna Japonica . . . .*

Teplov, E.N. and V.P. Teplov. 1947. Znachenie snezhnogo pokrova v ekologii mlekopitayushchikh i ptits Pechorsko-Ilychskogo gos. zapovednika (Importance of snow cover in the ecology of mammals and birds of Pechora-Ilych state preserve). *Tr. Pechorsko-Ilychsk. Gos. Zapovedn.*, no. 5.

Teplov, V.P. 1938. Volk v Kavkazskom zapovednike (Wolf in Caucasian preserve). *Tr. Kavkazsk. Gos. Zapovedn.*, vol. 1.

Teplov, V.P. 1948. O prichinakh gibeli losei i faktorakh, vliyayushchikh na ee intensivnost' (Causes of mortality in elk and factors affecting its intensity). *Zool. Zhurn.*, vol. 27, no. 1.

Teplov, V.P. 1953. Opyt otsenki khishchnicheskoi deyatel'nosti burogo medvedya (po materialam sobrannym v zapovednikakh) [Evaluating the predatory activity of brown bear (from data collected in preserves)]. Sb. *Preobrazovanie Fauny Pozvonochnykh Nashei Strany* (*Biotekhnicheskie Meropriyatiya*). Moscow.

Teplov, V.P. 1955. K zimnei ekologii rosomakhi v raione Pechoro-Ilychskogo zapovednika (Winter ecology of wolverine in Pechora-Ilych preserve). *Byull. Mosk. Ob-va Ispyt. Prirody. Otd. Biol.*, vol. 60, no. 1.

Teplov, V.P. and E.N. Teplov. 1947. Mlekopitayushchie Pechorsko-Ilychskogo zapovednika (Mammals of Pechora-Ilych preserve). *Tr. Pechorsko-Ilychsk. Gos. Zapovedn.*, no. 5.

Terletskii, P.E. 1932. Severnoe olenevodstvo (Reindeer husbandry). *Sb. Po Olenevodstvu. Tundrovoi Veterinarii i Zootekhn.* Moscow.

Ternovskii, D.A. 1929. Neskol'ko slov o faune i flore Belgorodskogo kraya v XVII v. (Some information on the fauna and flora of Belgorod territory in the seventeenth century). *Izv. Kursk. Ob-va Kraeved.*, nos. 4–6 (10–12), July and September, 1928.

Thomas, O. 1889. Mammals. The zoology of the Afghan Delimitation Commission. *Trans. Zool. Soc., London,* ser. 2, vol. 5, pt. 3.

Tikhomirov, B.A. 1937. *Arctophila fulva* (Trin.) And., ee ekologicheskie osobennsoti i kormovoe znachenie [*Arctophila fulva* (Trin.) And., its ecological characteristics and food importance]. *Tr. Dal'nevost. Fil. AN SSSR,* no. 2. Vladivostok.

Tikhomirov, B.A. 1955. Vliyanie obskogo lemminga (*Lemmus obensis* Brants) na rastitel'nyi pokrov tundry [Effect of Ob' lemming (*Lemmus obensis* Brants) on the vegetative cover of the tundra]. *Dokl. AN SSSR,* vol. 104, no. 4.

Timofeev, V.V. 1949. Zveri nashei oblasti (Animals of our Districts) Irkutsk.

Tolstoi, A.K. 1906. Dva dnya v Kirgizskoi stepi (Two days in Kirgizian steppes). *Vestn. Evropy.* February.

Torchinskii, I.A. 1902. Ob ovodakh iz roda *Oestromya* i o lichinkakh ovodov iz kozhi saigi i dzheirana (Gadflies from genus *Oestromya* and gadfly larvae from the skin of saiga and goitered gazelle). *Ezhegod. Zool. Muzeya Akad. Nauk,* vol. 7.

Trippensee, R.E. 1948. *Wildlife Management. Upland Game and General Principles.* New York.

Trippensee, R.E. 1953. *Wildlife Management. Fur-bearers, Waterfowl, and Fish.* New York, vol. 2.

Troitskii, V.N. 1930. Okhotnichii promysel Chuno-Angarskogo raiona, byvsh. Kanskogo okruga (Game hunting in Chuna-Angara region, former Kansk zone). *Izv. Sib. Kraev, Nauchn. Okhotn.-Prom. Stants.,* no. 1. Novosibirsk.

Trubetskoi, P.S. 1910. Buz-i-markhur, bukharskii shtopornyi kozel (Buz-i-markhor, Bukhara screw-horned goat). *Priroda i Okhota,* no. 1.

Tsalkin, V.I. 1944. K biologii razmnozheniya nastoyashchikh olenei (Reproductive biology of red deer). *Zool. Zhurn.,* vol. 23, no. 6.

Tsalkin, V.I. 1945. Materialy k izucheniyu rogov u nastoyashchikh olenei (*Cervus elaphus* L.) [Study of the antlers of red deer (*Cervus elaphus* L.)]. *Zool. Zhurn.,* vol. 24, no. 4.

Tsalkin, V.I. 1945. Vintorogii kozel SSSR (Markhor in the USSR). *Uch. Zap. Mosk. Gos. Un-ta,* no. 83, *Biologiya, mater. po Faune Turkmenii.*

Tsalkin, V.I. 1945. O vertikal'nom rasprostranenii dikikh baranov (Vertical distribution of wild sheep). *Byull. Mosk. Ob-va Ispyt. Prirody, Otd. Biol.,* vol. 50, nos. 1–2.

Tsalkin, V.I. 1946. K izucheniyu lin'ki u nastoyashchikh olenei (Study of molt in red deer). *Zool. Zhurn.,* vol. 25, no. 2.

Tsalkin, V.I. 1947. Sistematika kabargi (Systematics of musk deer). In *Oleni SSSR (Sistematika i Zoogeografiya)* by V.G. Heptner and V.I. Tsalkin, Moscow.

Tsalkin, V.I. 1948. Vintorogii kozel (Markhor). *Okhrana Prirody,* vol. 3.

Tsalkin, V.I. 1948. Diki baran v Turkmenii (Wild sheep in Turkmenia). *Byull. Mosk. Ob-va Ispyt. Prirody, Otd. Biol.,* vol. 53, no. 1.

Tsalkin, V.I. 1948. O sokrashchenii areala i chislennosti dikikh baranov (Range reduction and population decrease in wild sheep). *Okhrana Prirody,* vol. 2.

Tsalkin, V.I. 1948. O rosta rogov i stroenii cherepa u dikikh baranov (Horn growth and skull structure of wild sheep). *Zool. Zhurn.,* vol. 27, no. 5.

Tsalkin, V.I. 1950. Sibirskii gornyi kozel (Siberian ibex). *Mater. k Poznan. Fauny i Flory SSSR, Nov. Ser., Otd. Zool.,* no. 21, p. 36.

Tsalkin, V.I. 1951. Gornye barany Evropy i Azii (Mountain sheep of Europe and Asia). *Mater. k Poznan. Fauny i Flory SSSR, Nov. Ser., Otd. Zool.,* no. 27, p. 42.

Tsalkin, V.I. 1951. K istorii litovskogo zubra (History of Lithuanian wisent). *Dokl. AN SSSR, Nov. Ser.,* vol. 77, no. 2.

Tsalkin, V.I. 1954. Domashnie i dikie zhivotnye iz Skifskogo Neapolya (Domestic and wild animals from Skifsk Neapol). *Zhurn. Sov. Arkheologiya,* vol. 20.

Tsalkin, V.I. 1955. Izmenchivost' i istematika turov Zapadnogo Kavkaza (Caprinae, Artiodactyla) [Variation and systematics of west Caucasian tur (Caprinae, Artiodactyla)]. *Byull. Mosk. Ob-va Ispyt. Prirody, Otd. Biol.* vol. 60, no. 4.

Tsalkin, V.I. 1956. Materialy dlya istorii skotovodstva i okhoty v drevnei Rossi (Data on the history of cattle breeding and hunting in medieval Russia). Sb. *Mater. k Issled. po Arkheol. SSSR,* no. 51. Izd. AN SSSR.

Tsvetaeva, N.P. 1941. Bolezni zhivotnykh Moskovskogo zooparka (Diseases of animals of Moscow Zooligical Park). *Tr. Mosk. Zooparka,* vol. 2, no. 2.

Tugarinov, A.Ya., N.A. Smirnov and A.I. Ivanov. 1934. Ptitsy i mlekopitayushchie Yakutii (Yakutian birds and mammals). *Tr. SOPS Yakutskaya ASSR,* no. 6.

Turchkov, F. 1930. Okhotnichii promysel V.-Kam'ya (Game hunting in eastern Kam'ya). *Ural'skii Okhotnik,* nos. 6–7.

Turkin, V.N. and K.A. Satunin. 1900–1902. Zveri Rossii (Animals of Russia). Moscow, vols. 1–4.

Turov, I.S. 1953. O roli slepnei v biologii losya (Role of horseflies in the biology of elk). *Zool. Zhurn.,* vol. 32, no. 5.

Turov, S.S. 1932. Po vostochnomu otdelu Kavkazskogo gos. zapovednika. Otchet o rabote zoolog. eksped. 1930 g. (Eastern division of Caucasian state preserve. Account of work of 1930 zoological expedition). *Tr. Kavkazsk. Gos. Zapovedn.* Maikop.

Turov, S.S. and N.V. Kuznetsov. 1948. Zoologicheskie nablyudeniya vo vremya obrazovaniya Rybinskogo vodokhranilishcha (Zoological observations during the construction of Rybinsk water reservoir). *Okhrana Prirody,* vol. 6.

Tyulin, A.N. 1938. Promyslovaya fauna ostrova Belogo (Game fauna of Belyi Island). *Tr. N.-I. In-ta Polyarn. Zemledeliya, Ser. Promysl. Khozyaistvo,* no. 1.

Uraleva, V., Yu. Isakov, E. Gubina and A. Shapovalov. 1957. O vozmozhnoi roli saigakov v podderzhanii ochagov brutselleza v usloviyakh Astrakhanskoi oblasti (The possible role of saiga in sustaining brucellosis pockets under Astrachan' district conditions). *Tez. Dokl. Konfer. po Prirodnoi Ochagovosti i Epidemiologii.* Saratov.

Ushakov, G.E. 1953. Po nekhozhenoi zemle (On Virgin Soil). Moscow-Leningrad.

Ushkov, S.L. 1947. Promyslovaya fauna Il'menskogo gos. zapovednika (Game fauna of Il'men state preserve). *Tr. Il'mensk. Gos. Zapovedn.*, no. 3, pt. 1.

Ushkov, S.L. 1954. Perekhody kosuli na yuzhnom urale (Migrations of roe deer in southern Ural). *Byull. Mosk. Ob-va Ispyt. Prirody, Otd. Biol.*, vol. 59, no. 5.

Usov, S.A. 1859. Zubr (Wisent). *Vestn. Est. Nauk,* no. 6.

Usov, S.A. 1865. Zubr (Wisent). *Zap. Russk. Ob-va Akklimatizatsii.* Moscow.

Uspenskii, S.M. 1958. Bogatstva i okhrana zhivotnogo mira Sovetskoi Arktiki (Abundance and conservation of fauna of the Soviet Arctic). In Sb. *Probl. Severa,* no. 1. Moscow.

Vakulenko-Snigirevskaya. 1940. E.M. Kratkii obzor mlekopitayushchikh basseina r. Maloi Almatinki Almaatinskogo gos. zapovednika (Brief review of mammals of Little Almatinka River in Alma-Atinsk state preserve). *Tr. Almaatinsk. Gos. Zapovedn.*, no. 2.

Van den Brink, F.H. 1958. Die Säugetiere Europas westlich des 30 Längengrades. In *Ubersetzt und Bearbeitet* by Th. Haltenorth. Hamburg-Berlin.

Vasenko, E.P. 1950. Ekologiya i rasprostranenie saigi (Ecology and distribution of saiga). *Tr. Zapovedn. Barsa-Kel'mes,* no. 1.

Vendland, O.V. 1938. Kormovye rasteniya dikogo pyatnistogo olenya (Food plants for wild sika). *Vestn. Dal'nevost. Fil. AN SSSR,* no. 28, p. 1.

Vereshchagin, N.K. 1938. Sovremennoe sostoyanie dzheirana i Mil'sko-Karabakhskoi stepi (Present state of goitered gazelle in relation to Mil'sk-Karabakh steppe). *Izv. Azerbaidzhansk. Fil. AN SSSR,* no. 2.

Vereshchagin, N.K. 1938. Dagestanskii tur v Azerbaidzhane (Dagestan tur in Azerbaijhan). *Tr. Zool. In-ta Azerbaidzhansk. Fil. AN SSSR,* vol. 9, p. 45.

Vereshchagin, N.K. 1939. Dzheiran v Azerbaidzhane (Goitered gazelle in Azerbaijhan). *Tr. Zool. In-ta Azerbaidzhansk. Fil. AN SSSR,* vol. 10.

Vereshchagin, N.K. 1940. Dzheiran v Azerbaidzhane (Goitered gazelle in Azerbaijhan). *Priroda,* no. 4.

Vereshchagin, N.K. 1947. Okhotnich'i i promyslovye zhivotnye Kavkaza (Game and Hunting Animals of the Caucasus). Baku.

Vereshchagin, N.K. 1948. Los' *Alces* sp. kak nedavno vymershee zhivotnoe na Kavkaza (Elk *Alces* sp. as a recently extinct animal in the Caucasus). *Dokl. AN Azerbaidzhansk. SSR,* vol. 4, no. 3.

Vereshchagin, N.K. 1949. K istorii i sistematicheskomu polozheniyu losya (Mammalia, Ungulata) na Kavkaze [History and systematic position of elk (Mammalia, Ungulata) in the Caucasus]. *Dokl. AN SSSR, Nov. Ser.*, vol. 66, no. 3.

Vereshchagin, N.K. 1954. Baikal'skii yak (*Phoepagus* [sic] *baicalensis* N. Ver. sp. nova, Mammalia (iz pleistotsenovoi fauny Vostochnoi Sibiri [Baikal yak (*Poëphagus baicalensis* N. Ver. sp. nova, Mammalia) from Plesitocene fauna of eastern Siberia] *Dokl. AN SSSR, Nov. Ser.*, vol. 99, no. 3.

Vereshchagin, N.K. 1955. Kavkazskii los' (*Alces alces caucasicus* N. Ver. subsp. nova) i materialy k istorii losei na Kavkaze [Caucasian elk (*Alces alces caucasicus* N. Ver. subsp. nova) and information on the history of elk in the Caucasus]. *Zool. Zhurn.*, vol. 34, no. 2.

Vereshchagin, N.K. 1956. O prezhnem rasprostranenii nekotorykh kopytnykh v raione smykaniya evropeisko-kazakhstanskikh i tsentral'noaziatskikh stepei (Former distribution of some ungulates in the intrazonal area of European Kazakhstan and Central Asiatic steppes). *Zool. Zhurn.*, vol. 35, no. 10.

Vereshchagin, N.K. and V.I. Naniev. 1949. Prezhnee i sovremennoe rasprostranenie kopytnykh v Severnoi Osetii. 1. Vymershie vidy (Former and present distribution of ungulates in northern Osetia. 1. Extinct species). *Zool. Zhurn.*, vol. 28, no. 3.

Vereshchagin, N.K. and O.I. Semenov-Tyan-Shanskii. 1948. Ostatki kopytnykh v svyatlishchakh Severnoi Osetii (Remains of ungulates in northern Osetian sanctuaries). *Priroda*, no. 9.

Vetlitsin, P.I. 1894. Ob okhotnich'em promysle v okrastnostyakh g Khabarovska i o merakh k ego ukrepleniyu (Game hunting in the environs of Khabarov town and measures for strengthening it). *Priamurskie Vedomosti*, no. 40 (Appendix). Khabarovsk.

Vetulani, T. 1928. Weitere Studien über den polnischen Konik Polnisches Landpferd. *Bull. Intern. de l' Acad. Polon. des Sc. et des Lettres. Cl. des Sc. math. et Nat., Serie B. Sc. natur.*, no. 7, 1927. Cracovie.

Vetulani, T. 1936. Die Wiedereinführung des Waldtarpans in den Urwald von Bialowieza (Bialowies). Ibid., nos. 3-4, vol. 11. Cracovie.

Vietingoff, A.F. 1952. Die Bedeutung des Schwarzwildes bei Gradation der forst-schädlicher Insekten, *Fortwissenschaftliches Centralblatt*, vol. 17, nos. 1/2.

Vinitskii, V. 1937. Kopytnye na Urale (Ungulates in the Urals). *Boets-Okhotnik*, no. 9.

Vinogradov, A.F. 1871. Zubr (*Bison europaeus*) severo-zapadnogo Kavkaza [Wisent (*Bison europaeus*) of northwest Caucasus]. *Tr. Vtorogo S''ezda Russk. Estestvoisp. v Moskve*, pt. 2.

Vinogradov, A.F. 1872. Zubr severo-zapadnogo Kavkaza (Wisent in northwest Caucasus). *Okhoty i Konnozavodstva*, nos. 7–8.

Vinogradov, M.P. 1936. O srokakh otela i gona v olenevodstve (Fawning and rut periods in reindeer husbandry). *Sov. Olenevodstv.*, no. 6.

Vitovich, V. 1928. Tur i okhota na nego v Azerbaidzhane (Tur and its hunting in Azerbaidzhan). *Okhotnik*, no. 11.

Vitovich, V. 1928. Dzheiran v Azerbaidzhane (Goitered gazelle in Azerbaidzhan). *Zhurn. Okhotnik*, no. 6.

Volf, I. 1958. Pour le sauvetage des Chevaux de Przevalskii (*Equus przewalskii* Poljakov, 1881). *Mammalia*, vol. 22, no. 4. Paris.

Volovich, G.B. 1867. Reviziya pushch i pereborov zverinykh v byush. Velikom knyazhestve Litovskom i t. d. (A Survey of Dense Forests for Animals in the Former Lithuanian Great Empire, etc.). Izd. Vilensk. Arkheograf. Komissii. Vil'nyus.

Voloshko, B. 1958. Otradnoe yavlenie (A gratifying phenomenon). *Okhota i Okhot, Khoz.*, no. 3.

Von Hern, V. 1891. Zoograficheskie zametki po Akmolinskomu uezdu (Zoogeographic Notes on Akmolinsk District). Semipalatinsk.

Von Hern, V. 1905. Ob okhote v Semipalatinskoi oblasti (Hunting in Semipalatinsk district). *Okhotnich'ya Gazeta*, nos. 43–44.

Vrangel'—see Wrangel.

Vrublevskii—see Wroblewski.

Vsevolodov, B.P. and S.N. Boev. 1948. Patologo-morfologicheskie izmeneniya v legkikh gornykh kozlov i arkharov pri sinteokaulinozakh (Pathological and morphological changes in the lungs of mountain goat and argali sheep during syntheocaluesis). *Izv. AN Kazakhsk. SSR*, no. 43, *Ser. Parazitolog.*, no. 5.

Vysotskii, B.V. and V.G. Red'kina. 1954. Nekotorye dannye o khranitelykh patogennykh leptospir v prirode (Some data on hosts of pathogenic Leptospirea in nature). *Soobshch. Dal'nevost. Fil. AN SSSR*, no. 6.

Weber, M. 1927–1928. *Die Säugetiere.* Jena, vol. 1, 1927; vol. 2, 1928.

Westman, H. 1958. Algens skadegörelse på ungskogen. Kgl. Skogshögskoln.

Wrangel, F. 1841. Puteshestvie po severnym beregam Sibiri i po Ledovitomu moryu, sovershennoe v 1820, 1821, 1822, 1823, 1824 gg. ekspeditsiyu, sostoyavsheyu pod nachl' stvom Ferdinanda fon Vrangelya (Travels along the Northern Siberian banks and Arctic Ocean in 1820, 1821, 1822, 1823, and 1824 by the Expedition Constituted under the Leadership of Ferdinand von Wrangel). St. Petersburg, pts. 1–2.

Wrangel, F. 1948. Ibid., 2nd ed.

Wroblewski, K. [Vrublevskii]. 1908. Tripanozoma zubrov Belovezhskoi Pushchi (Trypanosomiasis among Belovezh Forest wisent). *Arkhiv. Veterin. Nauk.*, vol. 6. St. Petersburg.

Wroblewski, K. [Vrublevskii]. 1912. Teoreticheskaya differentsirovka nekotorykh zhvachnykh na drevesnoy-adnykh (Fruticivora) i travoyadnykh (Herbivora) i prakticheskoe ee znachenie (Theoretical differentiation of some Frugivora and Herbivora and its practical significance). *Arkhiv. Veterin. Nauk.,* vol. 8. St. Petersburg.

Wroblewski, K [Vrublevskii]. 1927. *Zubr Puzczy Bialowieskiej.* Monografja, Poznan.

Yakovlev, B.P. 1926. Zhivotnyi mir Man'chzhurii. Mlekopitayushchie (Animal world of Manchuria. Mammals). *Tr. Ob-va Izuch. Man'chzhurskogo Kraya, Ser. Estestvozn.,* A. no. 10. Kharbin.

Yakovlev, E.O. 1930. K granitsam rasprostraneniya promyslovykh zverei i ptits v Turukhanskom krae (Boundaries of distribution of game animals and birds in Turukhansk territory). *Tr. Zool. Sektsii Sredne-Sibirsk. Otd. Russk. Geograf. Ob-va, Zool. Sb.* Krasnoyarsk.

Yakushev, M. 1958. Losi v Biryuch'em lesu (Elk in Biryuchii forest). *Komsomol'skoe plemya,* September 7. Orenburg.

Yankovskii. 1882. Pyatnistye oleni, barsy i tigry Ussuriiskogo kraya (Sika, snow leopard, and tiger in Ussuri territory). *Izv. Vost.-Sib. Otd. Russk. Geograf. Ob-va,* vol. 13, no. 3. Irkutsk.

Yanushevich, A.I. 1950. Promyslovye zveri i ptitsy Zapadnoi Sibiri i okhota na nikh (Game Animals and Birds of Western Siberia and Their Hunting). Om'sk.

Yanushevich, A.I. 1952. Fauna pozvonochnykh Tuvinskoi oblasti (Vertebrate Fauna of Tuva Region). Novosibirsk.

Yanushevich, A.I. and I. Blagoveshchenskii. 1952. Promyslovye zveri i ptitsy Zapadnoi Sibiri (Game Animals and Birds of Western Siberia). Novosibirsk, 2nd ed.

Yanushko, P.A. 1955. Muflony (*Ovis musimon* Pall.) Krymskogo zapovednika [Mouflon (*Ovis musimon* Pall.) in Crimean preserve]. *Tr. Krymsk. Fil. AN USSR,* vol. 9, *Zool.,* no. 3. Simferopol'.

Yanushko, P.A. 1957. Stroenie i fiziologicheskie izmeneniya polovykh zhelez krymskikh olenei v razlichnye sezony goda (Structure and physiological changes in the sex glands of Crimean deer in different seasons of the year). *Tr. Krymsk. Gos. Zapovedn.,* vol. 4. Simferopol'.

Yanushko, P.A. 1957. Chislennost' i metody ucheta olenei v Krymskom zapovednike (Population and methods of counting deer in Cremean preserve). *Zool. Zhurn.,* vol. 36, no. 10.

Yanushko, P.A. 1957. Obraz zhizni krymskikh olenei i ikh vliyanie na estestvennoe lesovozobnovlenie (Life of Crimean deer and its effect on natural forest restoration process). *Tr. Krymsk. Gos. Zapovedn.,* vol. 4, Simferopol'.

Yanushko, P.A. 1958. Dinamika chislennosti krymskikh olenei

(Population dynamics of Crimean deer). *Zool. Zhurn.*, vol. 37, no. 8.

Yavlonskii, I. 1875. Primorskaya i stepnaya okhota v Astrakhanskoi gubernii (Coastal and steppe hunting in Astrakhan' province). *Okhota,* vol. 11, no. 2.

Yukhnev, L.M. 1903. Kochevniki Gornogo Altaya (Nomads of Montane Altai). Barnaul.

Yurgenson, P.B. 1935. Los' v tsentral'nykh raionakh Evropeiskoi chasti SSSR (Elk in central regions of the European part of the USSR). In *Los' i Ego Promysel* by P.B. Yurgenson et al. Moscow.

Yurgenson, P.B. 1938. Materialy k poznaniyu mlekopitayushchikh Priteletskogo uchastka Altaiskogo gos. zapovednika (Study of mammals of Telets section of Altai state preserve). *Tr. Altaisk. Gos. Zapovedn.,* no. 1.

Yurgenson, P.B. 1953. Nauchnaya laboratoriya v taige (Scientific laboratory in the taiga). *Priroda,* no. 8.

Yurgenson, P.B. 1955. K ekologii rysi v lesakh srednei polosy SSSR (Ecology of lynx in forests of the central zones of the USSR). *Zool. Zhurn.,* vol. 34, no. 3.

Yurgenson, P.B. 1957. Rasselenie okhotnich'ikh zverei dlya tselei sportivnoi okhoty v srednei polose (Colonization of game animals for purposes of sport hunting in the central zone). *Byull. Nauch.-Tekhn. Inform. Vses. N.-I. In-ta Lesovod. i Mekhanizatsii Lesn. Khoz.,* no. 5.

Yurgenson, P.B., L.G. Kaplanov and A.A. Knize. 1935. Los' i ego promysel (Elk and Its Hunting). Moscow.

Zablotskaya, L.V. 1957. Pitanie i estestvennye korma zubrov (Feeding and natural food of wisent). *Tr. Priroksko-Terrasn. Zapovedn.,* vol. 1.

Zablotskii, M.A. 1939. Tridtsat' pyat' let razvedeniya zubrov i ikh gibridov v zooparke Askaniya-Nova (1902–1937) (Thirty-five years of raising wisent and their hybrids in Askaniya-Nova Zoological Park, 1902–1937). Sb. *Kavkazsk. Zubr.* Moscow.

Zablotskii, M.A. 1947. Sovremennye zubry Belovezhskoi Pushchi (Present-day wisent of Belovezh Forest). *Nauch.-Metod. Zap. Gl. Upr. po Zapovedn.,* no. 9.

Zablotskii, M.A. 1949. Neobkhodimost' izucheniya osobennostei zubra i ego vosstanovlenie v SSSR (Need for studying the characteristics of wisent and its restoration in the USSR). *Nauch.-Metod. Zap. Gl. Upr. po Zapovedn.,* no. 13.

[Zablotskii, M.A.]. 1956. Gosudarstvennaya plemennaya kniga zubrov i bizonov (chistokrovnykh, chistoporodnykh i gibridnykh) [State Pedigree Book of Wisent and Bison (Purebreds, Thoroughbreds, and Hybrids). Moscow, vol. 1.

Zablotskii, M.A. 1957. Nekotorye biologicheskie osobennosti zubra i ikh izmenenie v usloviyakh zagonnogo soderzhaniya (Some biological characteristics of wisent and their variations under conditions of captive raising). *Tr. Prioksko-Terrasn. Zapovedn.*, vol. 1.

Zablotskii. M.A. 1957. Zagonnoe soderzhanie, kormlenie i transportirovka zubrov (instruktsiya) [Captive Breeding, Feeding, and Transport of wisent (Instructions)]. Moscow.

Zablotskii, M.A. 1957. Sistema meropriyatii, napravlennykh k bystreishemu vosstanovleniyu zubra v SSSR (Measures for the rapid restoration of wisent in the USSR). Sb. *Voprosy Ekologii*, vol. 2. Kiev.

Zalesskii, P.M. 1930. Maralovodstvo v severo-zapadnom Altae (Maral breeding in northwest Altai). *Tr. Ob-va Izuch. Sibiri i ee Proizvodit. Sil*, no. 3, *Maralovodstvo v Sibirsk. Krae.* Novosibirsk.

Zalesski, P.M. 1934. Proshloe i sovremennoe rasprostranenie kopytnykh v Zapadno-Sibirskom krae (Past and present distribution of ungulates in western Siberian region). *Okhotnik Sibiri*, nos. 7–8.

Zaletaev, V.S. 1956. Dzheiran, saigak i zayats-tolai na vostochnom poverezh'e Kaspiya (Goitered gazelle, saiga, and Tolai hare on the east bank of the Caspian). *Priroda*, no. 2.

Zappe, E. 1958. Zur Bedutung des Schwarzwildes bei Schadinsektengradationen im Walde. *Forst und Jagd.*, vol. 8, no. 1.

Zarovnyaev, A. 1933. K voprosu o migratsii promyslovykh zhivotnykh Yakutskogo Severa (Migration of game animals of northern Yakutia). *Sov. Yakutiya*, no. 9.

Zarudnyi, N.A. 1914. Koe-chto o prirode pustyni Kyzyl-Kum i ee faune (Some information about the nature of Kyzylkum desert and its fauna). *Izv. Turkestansk. Otd. Russk. Geograf. Ob-va*, vol. 10, no. 1.

Zarudnyi, N.A. 1915. Kratkii ocherk okhotnich'ego promysla v Syr-Dar'inskoi oblasti (Brief outline of game hunting in Syr-Darya district). *Turkestansk. Sel'sk. Khoz.*, nos. 7-8, Tashkent.

Zarudnyi, N. and S. Bil'kevich. 1918. Primechanie N. Zarudnogo i S. Bil'kevicha (Comments of Zarudnyi and Bil'kevich). See S. Bil'kevich, 1918.

Zavalishin, I. 1867. Opisanie Zapadnoi Sibiri (Description of western Siberia). *Sibirskaya Kirgizskaya Step'*. Moscow, vol. 3.

Zedwitz, F.H. 1937. *Die Gemse. Zentralbl. f. Kleintierk u. Pelztierk, Kleintier und Peltztier.* Leipzig, vol. 7.

Zharkov, I.V. 1940. Zimnii uchet kopytnykh progonom v Kavkazskom zapovednike (Winter counting of ungulates by driving them in

Caucasian preserve). *Nauch.-Metod. Zap. Gl. Upr. po Zapovedn.,* no. 6.

Zharkov, I.V. 1940. Rezul'taty ucheta zhivotnykh v Kavkazskom zapovednike v 1939 g. (Results of counting animals in Caucasian preserve in 1939). *Nauch.-Metod. Zap. Gl. Upr. po Zapovedn.,* no. 7.

Zharkov, I.V. 1952. Osnovnye metody ucheta dikikh kopytnykh (Major census methods for wild ungulates). Sb. *Metody Ucheta Chislennosti i Geograficheskogo Raspredeleniya Nazemnykh Pozvonochnykh.* Moscow.

Zharkov, I.V. 1954. Osobennosti letnego kormovogo rezhima losya v Zhigulyakh (Characteristics of summer feeding regime of elk in Zhiguli). *Byull. Mosk. Ob-va Ispyt. Prirody, Otd. Biol.,* vol. 59, no. 5.

Zharkov, I.V. 1957. Surovaya zima 1955–1956 gg. i ee vliyanie na olenei Voronezhskogo zapovednika (Severe winter of 1955–1956 and its effect on deer of Voronezh preserve). *Tr. Voronezhsk. Gos. Zapovedn.,* no. 7, Voronezh.

Zharkov, I.V. 1959. O vzaimootnosheniyakh sern s domashnimi zhivotnym i na vysokogornykh pastbishchakh Severo-Zapadnogo Kavkaza (Interrelations of chamois with domestic animals and effect on alpine pastures of northwest Caucasus). *Tr. Kav.kazsk. Gos. Zapovednika,* no. 5. Maikop.

Zharov, V.K. 1958. Okhotnich'i zhivotnye Kemerovskoi oblasti (Game animals of Kemerov district). *Izv. Irkutsk. S.-Kh. In-ta,* no. 8 (*F-ta Zootekhn. i Okhotoved*).

Zheleznov, I. 1857. Saigachniki (Saiga breeders). *Otechestvennye Zapiski,* no. 5.

Zhirnov, L.V. 1958. K biologii kosuli Tsentral'nogo Tyan'-Shanya (Biology of central Tien Shan roe deer). *Uch. Zap. Mosk. Gor. Ped. In-ta im. V.P. Potemkina,* vol. 84, *Kafedra Zoologii,* no. 7.

Zhitkov, B.M. 1898. Materialy po faune mlekopitayushchikh Simbirskoi gubernii (Information on mammalian fauna of Simbirsk province). *Izv. Ob-va Lyubit. Est., Antrop. i Etnogr.,* vol. 36; *Dnevnik Zool. Otd.,* vol. 2, no. 8.

Zhitkov, B.M. 1904. Otchety ekspeditsii Russkogo geograficheskogo obshchestva na Kanin poluostrov v 1902 g. (Account of expedition of Russian Geographic Society into Kanin Peninsula in 1902). *Zap. Russk. Geograf. Ob-va po Obshch. Geografii,* vol. 41, no. 1.

Zhitkov, B.M. 1913. Poluostrov Yamal (Yamal Peninsula). *Zap. Russk. Geograf. Ob-va po Obshch. Geografii,* vol. 49.

Zhitkov, B.M. 1914. O losyakh Ussuriiskogo kraya (Elk of Ussuri territory). *Dnevnik Zool. Otd. Ob-va Lyubit. Est., Antrop. i Etnogr., Nov. Ser.,* vol. 2, no. 3.

Zhitkov, B.M. and S.A. Buturlin. 1901. Po Severu Rossii (In northern (Russia). *Zemlevedenie,* vol. 8, nos. 3-4.

Zhitnikov, M. 1900. Ornitologicheskie nablyudeniya na r. Atreke (Ornithological observations at Atrek River). *Psovaya i Ruzheinaya Okhota,* nos. 10, 11, and 12.

Zimina, R.P. 1953. Kratkii ocherk fauny mlekopitayushchikh i ptits raiona Tyan'shanskoi fiziko-geograficheskoi stantsii (Brief outline of fauna of mammals and birds of Tien Shan physiographic station region). *Tr. In-ta Geograffi, AN SSSR,* no. 56.

Zonov, B.V. 1931. Opisanie basseina r. Omolona (Description of Omolon River basin). Sb. *Mater. Partii po Issledov. r. Kolymy,* no. 4. Irkutsk.

Zubareva, V.I. 1940. Fauna Kieva 1000 let nazad (Fauna of Kiev 1,000 years ago). *Priroda,* no. 8.

Zubkov, A.I. 1935. Dikie oleni Novoi Zemli (Wild deer of Novaya Zemlya). *Tr. Arktichesk. In-ta,* vol. 22.

Zubkov, A.I. 1935. Olenevodstvo i olen'i pastbishcha na Novoi Zemle (Reindeer husbandry and reindeer pastures in Novaya Zemlya). *Tr. Arktichesk. In-ta,* vol. 22.

Zverev, M.D. 1948. K voprosu o bystrote bega nekotorykh zhivotnykh (Speed of running in some animals). *Tr. Alma-Atinsk. Gos. Zapovedn.,* vol. 7. Alma-Ata.

Zverev, M.D. and A.A. Keleinikov. 1947. Nablyudeniya nad migratsiei kopytnykh i drugikh zhivotnykh v Alma-Atinskom zapovednike (Observations on migrations of ungulates and other animals in Alma-Ata preserve). *Tr. Alma-Atinsk. Zapovedn.,* no. 4. Alma-Ata.

Zyablovskii, E. 1806. Statisticheskoe opisanie Rossiiskoi Imperii (Statistical Outline of the Russian Empire). St. Petersburg.

Zykov, I.V. 1949. K voprosu okhrany prirody Salairskogo kryazha (Conservation of nature in Salair ridge). *Okhrana Prirody,* vol. 8.

Index of Latin Names of Taxa* †

Achlis 299
aegagrus *see* Capra
Aegoceros 516
— argali 602
— falconeri 593
— montanus 655, 664
— musimon 607
— pallasii 571
Aepyceros 420, 422
Aepycerotinae 420
affinis *see* Cervus
africanus *see* Equus
ahu *see* Cervus
alaiana *see* Capra
alashanicus *see* Cervus
albicus *see* Capreolus
albirostris *see* Cervus
albula *see* Ovis
Alcelaphus 217
Alces 80, 99, *121*, 172, 174, 176, **217**, 300
— alces 77, 81, **220**, *222*, *224*, *227*, *230*, *232*, *235*, *238*, *245*, *250*, *255*, **255**, 256, *257*
— americanus 255, 256, 257
— angusticephalus 222, 255
— antiquorum 222, 255
— bedfordi 222, 256
— bedfordiae 222, 255, 256
— cameloides 222, *224*, **256**, *257*
— caucasicus 222, *232*, 255
— coronatus 255
— europaeus 222, 255
— gigas 77, 222, 255, 256, 257
— jubata 222, 255
— latifrons 220
— machlis 222, 255
— meridionalis 222, 255
— palmatus 222, 255
— pfizenmayeri 222, *255*, **255**, 256, 257
— tymensis 222, 255
— typicus 222, 255
— uralensis 222, 255
— yakutskensis 222, 255
alces *see* Alces, Cervus
alfredi *see* Cervus
alleni *see* Ovis
almasyi *see* Capra
alpium *see* Capra
altaica *see* Capra, Ovis, Procapra
altaicus *see* Cervus, Moschus
Amblypoda 18
americanus *see* Alces, Bison, Cervus, Oreamnos, Rangifer
Ammodorcas 420, 422
Ammon 602
ammon *see* Capra, Ovis
Ammotragus 457, 519, 606, 614
— lervia 457, 621
anatolica *see* Equus, Ovis
Anchitheriinae 695
Ancodonta 23
andamanensis *see* Sus
angasi *see* Strepsiceros
angusticephalus *see* Alces
angustirostris *see* Rangifer
Anoa 373, 374
— depressicornis 373
Anthracotherioidea 23
Antidorcas 418, 420, 422
Antilocapra 16, 75, 79
Antilocapridae 74, 75, 362, 364, 366
Antilocaprinae 75
Antilope 418, 420
— caudata 485, 487
— crispa 487, 493
— dorcas 423
— gazella 522
— goral 485, 487
— gutturosa 440, 441, 443
— orientalis 443
— persica 423
— saiga 457, 459
— scythica 459
— subgutturosa 423
Antilopinae 362, 366, 367, 417, 418, 419, *419*, 420, 455, 459
Antilopini 419, 420, 422, 455
antiquorum *see* Alces

---

*Reproduced from the Russian original. Page numbers of the Russian original appear in the left-hand margin in the text—General Editor.

† Page numbers with description are given in bold and those with illustrations, in italics.

arcticus *see* Moschus, Rangifer
Argali 602
argali *see* Aegoceros, Ovis
argaloides *see* Ovis
Aries 516, 602
aries *see* Ovis
arkal *see* Ovis
armeniana *see* Ovis
armenius *see* Capreolus
arnee *see* Bubalus
arnee-bubalus *see* Bubalus
arnouxianus *see* Nemorhaedus
Artiodactyla 10, 11, **15**, *17*, 674
Aschaeomeryx 364
asiatica *see* Rupicapra
asiaticum *see* Musimon
asiaticus *see* Cervus, Musimon, Rangifer
Asinus 696, 698, 718
asinus *see* Equus
atlanticus *see* Cervus
attila *see* Sus
auduboni *see* Ovis
Aulacochoerus 26
Axis 103, 106, 677
axis *see* Cervus

Babyrouza 25
bactrianus *see* Camelus, Cervus
baicalensis *see* Cervus, Poëphagus
bairdi *see* Tapirus
balcanica *see* Rupicapra
baleyi *see* Nemorhaedus
balticus *see* Capreolus, Cervus
barbarus *see* Cervus, Sus
barbatus *see* Sus
bedfordi *see* Alces, Capreolus
bedfordiae *see* Alces
bedfordianus *see* Cervus
berezovskii *see* Moschus
Bibos 374, 386
— frontalis 374
— gaurus 373
— javanicus-banteng 374
— sauveli 374
bicornis *see* Diceros
biedermanni *see* Cervus
Bison 374, 375, **385**, 386, *387*
— americanus 374
— bison 391
— bonasus 367, 371, 374, **388**, *389*, *392*, *396*, **397**
— caucasia 388
— caucasicus *396*, **398**
— europaeus 388, 397
— nostras 397
— palaeosinensis 386
— priscus 388
— sivalensis 386
— urus 397
bison *see* Bison, bos
blanfordi *see* Ovis
Blastocerus 174, 300
blythi *see* Capra
bocharensis *see* Ovis
Bonasus 385
bonasus *see* Bison, Bos
Boocerus 373
borealis *see* Ovis, Tarandus
Bos 373, **374**, 375, 378, 386
— bison 385, 388
— bonasus 385, 388
— caucasicus 388
— grunniens 367, 374, 382
— mutus 367, 373, 374, 375, **382**
— poëphagus 382
— primigenius 367, 372, 373, 374, 375, **376**, *376*, *377*, 378, 379
— taurus 367, 374, 375, 376
— trochoceros 378
Bos urus 388
Boselaphinae 373
Boselaphini 373
Boselaphus 362, 373, 374
— tragocamelus 373
Bovidae 74, 75, 82, **361**, 362, *363*, 364, 366, 367, 418, 606
Bovinae *365*, 366, 367, **371**, 372, 373, **418**, 454
Bovini 373, 374, 385, 386
Bovoidea 75, 361
brauneri *see* Cervus
Brontotheriidae 690
Bubalus 373, 386
— arnee 367
— arnee-bubalis 373
— bubalus 367, 374
— mindorensis 373
bubalis *see* Bubalus
Budorcas 457
— taxicolor 457
burchelli *see* Equus
buskensis *see* Rangifer

caballus *see* Equus
caboti *see* Rangifer
Caenolestoidea **9**
caffer *see* Syncerus
californiana *see* Ovis
Camelidae 70
Camelinae 70
cameloides *see* Alces
Camelus 70
— bactrianus 69, 70
— dromedarius 70
— knoblochi 69
campestris *see* Cervus
canadensis *see* Cervus, Ovis
Capella 498
capella *see* Rupicapra
Capra 188, 369, 457, **516**, *518*, **519**, 520, 521, 549, 552, 572, 606, 621
— aegagrus 369, 519, 520, 521, *522*, **523**, *527*, *528*, *529*, **529**, 530, *539*, 542, 568, 577, 596, 598, 599, 600
— alaiana 534, **550**, 551
— almasyi 534, 550, 551
— alpium 534
— altaica 534, 550
— ammon 602
— blythi 523, 530
— cashmeriensis 600
— caucasica 370, 516, 520, 523, 542, 549, **563**, *564*, *566*, *567*, 570, 573, 574, 575, *576*
— chialtanensis 521, 526, 600
— cretica 530
— cylindricornis 370, 519, 520, 521, 523, 525, 549, *567*, 569, 570, **571**, *572*, 575, *576*, 595, 596, 614, 621
— dementievi 551
— dinniki 565, 572, 575
— dorcas 420, 530
— falconeri 188, 369, 516, 520, 521, 523, 525, 526, *539*, 542, 549, 573, 574, **593**, *594*, *597*, *599*, 600
— fasciata 534, 550
— formosovi 536, 550, 551
— gazella 523
— hagenbecki 551
Capra heptneri 593, **600**
— hircus 516, 520, 521, 523
— ibex 516, 517, 520, 521, 523, 524, 542, 550, 574
— jerdoni 600
— lorenzi 534, 550
— lydekkeri 550
— megaceros 600
— merzbacheri 536, 550
— neglecta 530
— neglectus 523
— nubiana 520, 521, 529, 542, 574
— ognevi 593, 600
— pallasii 534, 550
— pictus 530
— prisca 519
— pyrenaica 517, 519, 520, 521, 572, 574, 596
— raddei 565, 570
— rupicapra 498, 501
— sakeen 534, 550, 551
— sayga 459
— severtzovi 520, 521, 563, 570, 572, 575
— sibirica 188, 370, 516, 520, 521, 524, 526, **534**, *535*, 536, *537*, *539*, *543*, *545*, *548*, **550**, 551, 568, 574, 596, 599
— sinaitica 520, 529
— tatarica 457, 459
— transalaiana 534, 550
— turcmenicus 523, **530**
— typica 534, 550
— walie 520
caprea *see* Capreolus
Capreolini 172
Capreolus 76, 80, 99, 172, **174**, *176*, 176, 300, 501
— albicus 178, 199
— armenius 179, 199, 200
— balticus 178, 199
— bedfordi 176, 178, **201**, 202
— caprea 178, 199
— capreolus 81, *172*, *176*, 176, *177*, **178** 179, *187*, *191*, **199**, 202
— caucasica 178
— caucasicus **201**
— europaeus *178*, 199
— ferganicus 178, 201
— mantschuricus 178, 201
— melanotis 201, 202
— ochracea 179, 201
— pygargus 176, 177, *180*, **200**, 202
— tianschanicus 178, **201**
— transsylvanicus 178, 199
— vulgaris 178, 199
— warthae 178, 199
— zedlitzi 179, 199

capreolus *see* Capreolus, Cervus
Capricornis 457, 487
— crispus 457
— sumatraensis 457
Caprina 485
Caprinae 366, 367, 418, 441, **453**, 454, 455, *456*, 457, 459, 572
Caprini 457, 487, 501, 519, 606
Caprovis 602
caribou *see* Rangifer
Carnivora 10, 11
carpatica *see* Rupicapra
carpaticus *see* Cervus
cartusiana *see* Rupicapra
cashmeriensis *see* Capra
caspicus *see* Cervus
castaneus *see* Equus
castillanus *see* Sus
caucasia *see* Bison
caucasica *see* Capra, Capreolus, Rupicapra
caucasicus *see* Alces, Bison, Bos, Capreolus, Cervus
caudata *see* Antilope
caudatus *see* Nemorhaedus
celebensis *see* Sus
Cemas 485, 498
— colus 459
Cephalophinae 366, 373
Ceratomorpha 691
Cervalces 220
Cervidae 72, 75, **76**, *78*, 79, 80, 82, 83, 172, 300, 362, 364, **674**
Cervinae 79, 80, **98**, 99, 100, *102*, 172, 176, 220, 300
Cervoidea 75, 76
Cervulinae 176
Cervus 80, 99, **100**, *102*, 103, 105, 106, 299, 304, 674, 677
— affinis 121, 143
— ahu 178
— alashanicus 143
— albirostris 103
— alces 222
— alfredi 100
— americanus 222
— asiaticus 122, 142
— atlanticus 143
— axis 103, 104
— bactrianus 122, 125, *131*, *137*, *141*, 143
— baicalensis 122, 142
— balticus 122
— barbarus 125, 143
— bedfordianus 122, 142
— biedermanni 122, 142
— brauneri 122, *137*, **140**
— campestris 122, 123, 140
— canadensis 121, 122, 142, 143
— capreolus 174, 178
— carpathicus 123, 140
— caspicus 122, 140
— caucasicus 122, 140
— coronatus 222
— corsicanus 125, 143
— dama 77, 81, 100, 101, 103, 104, **674**, *675*, *678*, *679*
— duvauceli 99, 103
— dybowskii 104, 109
— elaphus 77, *78*, 81, 99, 100, *102*, 103, 104, 105, 106, **121**, 122, 123, *124*, *127*, *128*, *131*, 134, *137*, *141*, 143
— eldi 103
— equinus 103
— eustephanus 122, 142
— grassianus 110
— guettardi 302
— hagenbecki 122, 143
— hanglu 143
— hippelaphus 121, *137*, **140**
— hispanicus 143
— hortulorum 104, *108*, **109**
— isubra 122, 142
— kalamianensis 103
— keramae 110
— kopschi 109
— kuhli 103
— lühdorfii 122, 142
— macneilli 143
Cervus major 104, 109
— mandarinus 110
— mantchuricus 104, 109, 110
— maral 121, 122, 125, 134, *137*, **140**, *141*
— merriami 143
— mesopotamica 678, 679
— montanus 122, 123, 134, *137*, **140**
— nannodes 143
— nippon 81, 100, **103**, *107*, *108*, 109, 127
— philippensis 100
— platyceros 674
— porcinus 103
— pseudaxis 104, 110
— pygargus 178
— rangifer 302

— schomburgki 99, 100, 103
— schottingi 302
— scoticus 143
— sibirica 122
— sibiricus 122, *124*, 125, 126, *137*, 142, 302
— sika 100, 103
— songarica 121
— songaricus *137*, *141*, 142
— taiouanus 100, 109
— tarandus 299, 302
— tauricus 122, 140
— timorensis 103
— typicus 104, 109
— unicolor 103
— vulgaris 122
— wachei 122, 142
— wallichi 100, 143
— xanthopygos 121, *137*, *141*, 142
Cetacea 10, 11
Chalicotheridae 690
chialtanensis *see* Capra
chirodontus *see* Sus
Chiroptera 10, 11
Choeropsis 21, 23
chrysogaster *see* Moschus
chukchensis *see* Tarandus
collium *see* Ovis
Colus 457
colus *see* Cemas
Condylarthra 18
Connochaetes 485
continentalis *see* Sus
coronatus *see* Alces, Cervus
corsicanus *see* Cervus
Cremnobates *see* Ovis
Creodonta 18
cretica *see* Capra
crispa *see* Antilope
crispus *see* Capricornis
cristatus *see* Sus
cycloceros *see* Ovis
cylindricornis *see* Capra, Ovis, Rangifer

dalli *see* Ovis
Dama 103
— mesopotamica 103
— schaeferi 101, 678
dama *see* Cervus, Gazella
Dasychoerus 26
dauricus *see* Ovis
davidianus *see* Elaphurus
dawsoni *see* Rangifer
dementievi *see* Capra
deperdita *see* Gazella
depressicornis *see* Anoa
Dermoptera 10
Diceros bicornis 691
— simus 687, 691
Didermoceros sumatrensis 691
dinniki *see* Capra
Diprotodontia 9
Dolichohippus 696, 716
dorcas *see* Antilope, Capra, Gazella, Rupicapra
Dorcatragus 420
Dorcelaphus 174
dromedarius *see* Camelus
Dromomerycinae 79
duvauceli *see* Cervus
dybowskii *see* Cervus

Edentata 10
Elaphoceros 100
Elaphodus 77, 80, 99, 176
Elaphurus 99, 101
— davidianus 77, 80, 304
Elaphus 100
— ussuricus 122
elaphus *see* Cervus
eldi *see* Cervus
Equidae 690, **693**, *694*, 695
Equiferi 716
Equiferus 716
equiferus *see* Equus
Equinae **696**
equinus *see* Cervus
Equoidea 693
Equus 695, **696**, *697*, 718
— africanus 688, 692, 695, 696, 718
— anatolica 707
— asinus 695, 698
— burchelli 691
— caballus 695, 698, 715, 721
— castaneus 698, 706
— equiferus 716
— ferus 716

— finschii 698, **706**
— gmelini 715, 718, **721**, 722
— grevyi 696
— hemionus 692, 696, 697, **698**, *699*, *701*, *705*, 705, **706**, 718
— hemippus 706, 707
— khur 707
— kiang 705, 707
— onager 698, *699*, 705, 716, 707
— przewalskii 691, 696, 697, **715**, 716, 718 *719*, 721, *722*, **722**
— quagga 691, 696
— silvatica 721, **722**
— stenonis 696
— sylvestris 716, 722
— tarpan 716
— zebra 691, 696
Eucapra 516
Eucervus 100
Eucladocerus 220
Euhys 26
Euibex 516
europaea *see* Rupicapra
europaeus *see* Alces, Bison, Capreolus, Sus
euryceros *see* Taurotragus
eustephanus *see* Cervus
Eutheria 10

falconeri *see* Aegoceros, Capra
falz-feini *see* Sus
fasciata *see* Capra
fennicus *see* Rangifer
Ferae 10
ferganicus *see* Capreolus
Ferungulata 10, 18
ferus *see* Equus
finschii *see* Equus
floresianus *see* Sus
formosovi *see* Capra
fricki *see* Rangifer
frontalis *see* Bibos
furcifer *see* Rangifer, Tarandus

gargantua *see* Sus
gaurus *see* Bibos
Gazella 418, 419, **420**, *421*, 422, 440
— dama 422
— deperdita 422
— dorcas 422
— gazella 422
— gracilicornis 423, 429
— granti 422
— leptoceros 422
— pelzelni 422
— reginae 429
— rufifrons 422
— sairensis 423
— seistanica 423
— soemmeringei 422
— spekei 422
— subgutturosa 368, 421, 422, *423*, **423**, *425*, *426*, *428*, 440
— thomsoni 422
— tilonura 422
— typica 423, 429
— yarcandensis 429
— gazella *see* Antilope, Capra, Gazella
Gazellinae 420
Gelocus 366
gigas *see* Alces, Rangifer, Sus
Giraffa 16, 75
Giraffidae 74
Giraffoidea 75
glama *see* Lama
Glires 10
gmelini *see* Equus, Ovis
goral *see* Antilope, Nemorhaedus
gracilicornis *see* Gazella
granti *see* Gazella
grassianus *see* Cervus
grevyi *see* Equus
griseus *see* Nemorhaedus
groenlandicus *see* Rangifer
grunniens *see* Bos
guanicoë *see* Lama
guettardi *see* Cervus, Rangifer
gutturosa *see* Antilope, Procapra

hagenbecki *see* Capra, Cervus
hanglu *see* Cervus
Harana 100
heinsii *see* Ovis
hemionus *see* Equus, Odocoileus
hemippus *see* Equus
Hemitragus 457, 519
— jemlahicus 457
heptneri *see* Capra
hippelaphus *see* Cervus
Hippocamelus 174
Hippomorpha 691
Hippopotamidae 23

Hippopotamus 16, 21, 23
Hippotigris 696, 718
Hippotraginae 366, 418
Hircus 516
hircus *see* Capra
hispanicus *see* Cervus
hodgsoni *see* Nemorhaedus, Ovis, Pantholops
hortulorum *see* Cervus
humei *see* Ovis
Hydropotes 72, 76, 77, 79, 174
Hydropotinae 79, 80, 99
Hyemoschus 71, 74
Hylarnus 420
Hylochoerus 25
Hypertragulidae 364
Hyracoidea 10
Hyracotheriinae 695

Ibex 516
— imberbis 459
— sibiricus 516, 534
idex *see* Capra
imberbis *see* Ibex, Strepsiceros
indicus *see* Tapirus
Insectivora 10, 11
Isectolophidae 690
isphaganica *see* Ovis
isubra *see* Cervus

jakutskensis *see* Rangifer
javanicus-banteng *see* Bibos
jemlahicus *see* Hemitragus
jerdoni *see* Capra
jubata *see* Alces, Ovis

kalamianensis *see* Cervus
karelini *see* Ovis
Kemas 485
— raddeanus 487
keramae *see* Cervus
khur *see* Equus
kiang *see* Equus
knoblochi *see* Camelus
Kobus 361
kopschi *see* Cervus
koreanus *see* Sus
kozlovi *see* Ovis
kuhli *see* Cervus

Lagomorpha 10, 11
lama 70
— glama 70
— guanicoë 70
— vicugna 70
lapponum *see* Rangifer, Tarandus
laristanica *see* Ovis
latifrons *see* Alces
lenaensis *see* Ovis
lenensis *see* Rangifer, Tarandus
Leptobos 373
leptoceros *see* Gazella
lervia *see* Ammotragus
leucomystax *see* Sus
Limnotragus 373
Lithocranius 420, 422
littledalei *see* Ovis
Lophiodontidae 690
lorenzi *see* Capra
lühdorfii *see* Cervus
lybicus *see* Sus
lydekkeri *see* Capra, Ovis

machlis *see* Alces
macneilli *see* Cervus
Madoqua 362, 420
Madoquinae 420
major *see* Cervus
majori *see* Sus
mandarinus *see* Cervus
mandchuricus *see* Sus
mantschuricus *see* Capreolus, Cervus
maral *see* Cervus
Marsupialia 10
Mazama 77, 174, 300
megaceros *see* Capra
Megaloceros 220, 677
melanotis *see* Capreolus
meridionalis *see* Alces, Sus
merriami *see* Cervus
Merychippus 696
merzbacheri *see* Capra
Mesaxonia 10, 18, 687
mesopotamica *see* Cervus, Dama
Metatheria 10
mexicana *see* Ovis
Microhippus 696
— tafeli 696
middendorfi *see* Ovis
mindorensis *see* Bubalus
mongolica *see* Ovis, Saiga
Monotremata 10
montanus *see* Aegoceros, Cervus,

Rangifer
Morenelaphus 300
moschatus *see* Ovibos
moschiferus *see* Moschus
Moschinae 79, 80, **81**, *82*, 83
Moschus 76, 79, 80, *82*, **83**
— altaicus 83, 90
— arcticus 83, 90
— berezovskii 83, 91
— chrysogaster 83
— moschiferus 80, *82*, **83** *87*, **90**
— parvipes 83, **90**
— sachalinensis **90**
— sibiricus 83, 90
— sifanicus 83
— turovi 83, 90
moupinensis *see* Sus
Muntjacinae 79, 80, 99
Muntjacus 77, 99, 176
— reevesi 77
Musimon 602, 606, 632
— asiaticus 602, 607
musimon *see* Aegoceros, Ovis
Mutica 10
mutus *see* Bos, Poëphagus
Mystacoceti 9

Nanger 422
nannodes *see* Cervus
nanus *see* Syncerus
nasonovi *see* Ovis
nayaur *see* Pseudois
neglecta *see* Capra
neglectus *see* Capra
nelsoni *see* Ovis
Nemorhaedini 457, 487
Nemorhaedus 457, **485**, *486*, 487, 501
— arnouxianus 493
— baleyi 493
— caudatus **493**
— goral 369, 457, 485, **487**, 488, *491*, 493
— griseus 487, 493
— hodgsoni 493
— raddeanus *491*
Neocervinae 174, 176, 300
Neotraginae 420
Neotragini 419, 420
Neotragus 16, 364, 420
Nesotragus 420
nicobaricus *see* Sus
nigrimontana *see* Ovis
nigripes *see* Sus
nippon *see* Cervus
nivicola *see* Ovis
nostras *see* Bison, Urus
Nototragus 420
Notoungulata 18
Novibos 374
nubiana *see* Capra
obscura *see* Ovis
ochracea *see* Capreolus
Odocoileinae 79, 80, 99, **172**, *173*, 174, 220, 300
Odocoileus 174, 300
— hemionus 151
Odontoceti 9
ognevi *see* Capra
Onager 696
onager *see* Equus
ophion *see* Ovis
Oreamnos 457, 487, 501
— americanus 457, 501
Oreodonta 23
Oreotraginae 420
Oreotragus 420
orientalis *see* Antilope, Ovis
ornata *see* Rupicapra
Orthaegoceros 516, 520
orys *see* Taurotragus
Ourebia 420
Ovibos 364, 453, 457
— moshatus 457
Ovibovinae 454
Ovibovini 457
Ouis 370, 455, 457, 459, 419, 572, **602**, *605*, 606, 621, 632
— albula 637, 664
— alleni 655, **664**
Ovis altaica 608, 637
— ammon 369, 370, 457, 572, 602, 604, *605*, 606, **607**, 608, 612, *613*, 614, 615, 616, *618* 618, 620, 621, *623*, 630, 632, *635*, **637**, 639, 640, 651, 659, 663, 666, 670,
— anatolica 638, 639
— argali 607, 608, 637
— argaloides 606
— aries 602, 607
— arkal 607, 608, 634
— arkar 608
— armeniana 609
— auduboni 665

— blanfordi 615, 639
— bocharensis 608, 612, 615, **633**, *635*, 644
— borealis 655, **664**
— californiana 665
— canadensis 370, 457, *605*, 607, 621, **655**, *657*, *661*, 663, 665, 672
— collium 608, 609, **637**
— cremnobates 665
— cycloceros 607, 608, 612, *613*, 615, 616, *618*, 618, 619, 620, 621, **634**, 636, 639, 649, 659
— cylindricornis 571
— dalli 607, 663, 664, 665
— dauricus 608, 637
— gmelini 608, 610, 611, *613*, 614, 616, *618*, 618, 620, 632, **633**, 639
— heinsii 608, 636
— hodgsoni 639
— humei 608, 637
— isphaganica 614, 638, 639
— jubata 639
— karelini 608, *613* **636**, 637, 640, 649, 652, 654, 663
— kenaiensis 663, 665
— kozlovi 639
— laristanica 614, 620, 632, 638, 639
— lenaensis 655, 664
— littledalei 608, 637
— lydekkeri 655, 656, **664**, 665
— mexicana 665
— middendorfi 655, 664
— mongolica 608, 637
— musimon 369, 602, 604, 610, 615, 616, 618, 619, 620, 632, **638**
— nassonovi 609, 636
— nelsoni 665
— nigrimontana 608, 618, **636**
— nivicola 602, 606, 655, 656, *657*, *658*, 659, 661, **663**, 665
— obscura 664
— ophion 572, 608, 609, 614, 618, 620, 621, 622, 632, 633, 638
— orientalis 607, *613*, 614, 616, 620, 632, 639
— polii 608, 609, 612, *613*, 614, 615, 616, 618, 619, 620, 621, 622, 627, 629, 632, 636, **637**, 638, 640
— potanini 664
— przevalskii 609, 637
— punjabensis 615, 620, 639
— sairensis 608, 637
— sawignii 606
— severtzovi 608, 616, 618, 620, 627, 628, **636**
— shantungensis 606
— stonei 663, 665
— storcki 655, 663
— tomensis 606
Ovis typica 608, 637
— urmiana *613*, 614, 638
— varenzovi 608, 634
— vignei 608, 614, 615, 620, 626, 627, 628, 632, **633**
— weemsi 665
— zdanskyi 606

Pachyceros 602, 606
Paenungulata 10
Palaeodonta 23
Palaeomerycinae 79
palaeosinensis *see* Bison
Palaeotheriidae 690, 693
Palaeotraginae 75
Palaeotragus 75
pallasii *see* Aegoceros, Capra
palmatus *see* Alces
Pantholopinae 454
Pantholopini 457
Pantholops 441, 455, 457, 459
— hodgsoni 457
papuensis *see* Sus
Paralces 217
Paraxonia 10, 15, 18
parva *see* Rupicapra
parvipes *see* Moschus
pearsoni *see* Rangifer
pearyi *see* Rangifer
Pecora 74, 75, 76
pelzelni *see* Gazella
Perissodactyla 10, 11, 18, 685, *689*, 691
persica *see* Antilope
pfizenmayeri *see* Alces
Phacochoerus 25
philippensis *see* Cervus
philippinensis *see* Rusa
Pholidota 10
phylarchus *see* Rangifer
picticaudata *see* Procapra
pictus *see* Capra
pinchaque *see* Tapirus
Pinnipedia 10, 11
platyceros *see* Cervus

platyrhynchus *see* Rangifer
Plesippus 696
Pliocervus 176
Pliohippus 696
Poëphagus 367, 374, 375, 382, 386
— baicalensis 385
— mutus 382, *383*, *384*
poëphagus *see* Bos
polii *see* Ovis
Polyprotodontia 9
porcinus *see* Cervus
Porcula 25, 26, 31
Potamochoerus 25, 26
potanini *see* Ovis
Primates 10
primigenius *see* Bos
prisca *see* Capra
priscus *see* Bison
Proboscidea 10
Procapra 418, 420, 422, **440**, 441, *441*, *442*
— altaica 443, 446
— gutturosa 368, 440, **441**, *442*, *444*
— picticaudata 440, 441
— przevalskii 441
Procapreolus 176
Procoileus 99
Prodorcas 440, 441
Prosimiae 9
Prototheria 10
Protragoceros 373
Protungulata 10
przevalskii *see* Procapra
Przevalskium 103, 106
przewalskii *see* Equus, Ovis
Pseudaxis 100
pseudaxis *see* Cervus
Pseudocervus 100
Pseudois 364, 457, 519, 606, 614
— nayaur 457, 621
Pudella 174
punjabensis *see* Ovis
Pudu 76, 77, 172, 174, 300
pygargus *see* Capreolus, Cervus
pyrenaica *see* Capra, Rupicapra

quadricornis *see* Tetraceros
quagga *see* Equus

raddeanus *see* Kemas, Nemorhaedus, Sus
raddei *see* Capra
Rangifer 76, 80, 172, 174, **299**, 300, *301*
— americanus 256
— angustirostris 304, 323
— arcticus 302, 303, 321, 322, 324
— asiaticus 303, 322
— buskensis 303, 323
— caboti 324
— caribou 302, 324
— cylindricornis 303, 321
— dawsoni 324
— fennicus 303, 321
— fricki 300
— furcifer 321
— groenlandicus 324
— guettardi 321
— jakutskensis 323
— lapponum 321
— lenensis 322
— montanus 324
— pearsoni 303, **322**
— pearyi 321, 322, 324
— platyrhynchus 321
— phylarchus 303, **323**
— schottingi 321
— setoni 304, 323
— sibiricus 303, **322**, 324
— silvicola 304, 321
— tarandus 81, 300, *301*, **302**, 303, *303*, *305*, *308*, *310*, *314*, **321**, 322
— terraenovae 324
— transuralensis 304
— typicus 303, 321
— valentinae 304, **322**, 323
rangifer *see* Cervus
Raphicerus 420
Reduncini 418
reevesi *see* Muntjacus
reginae *see* Gazella
reiseri *see* Sus
Rhinoceros sondaicus 691
— unicornis 688, 691
Rhinocerotidae 690, 695
Rhynchotragus 420
riukianus *see* Sus
Rodentia 10, 11
Rucervus 101, 103, 106
rufifrons *see* Gazella
Ruminantia 18, **71**, *73*, **74**, 364, 366
Rupicapra 361, 457, 485, 487, **498**, 499, 501
— asiatica 502, 507, 508
— balcanica 508
— capella 501

— carpatica 502, **508**
— cartusiana 508
— caucasica 502, *504*, **507**
— dorcas 502
— europaea 501
— ornata 508
— parva 508
— pyrenaica 508
— rupicapra 369, 457, *500*, **501**, 502, *504*, 508
— tragus 501, 502
rupicapra *see* Capra, Rupicapra
Rupicaprinae 454
Rupicaprini 457, 501, 519
Rusa 79, 103, 106, 677
— philippinensis 18

Saiga 455, **457**, *458*, 459
— mongolica 459, 465
— tatarica 368, 457, *458*, **459**, *463*, **465**
saiga *see* Antilope
Saiginae 454
Saigini 455, 457
sairensis *see* Gazella, Ovis
sakeen *see* Capra
salvanius *see* Sus
sachalinensis *see* Moschus
sauveli *see* Bibos
sawignii *see* Ovis
sayga *see* Capra
schaeferi *see* Dama
schomburgki *see* Cervus
schottingi *see* Cervus, Rangifer
scoticus *see* Cervus, Urus
scriptus *see* Strepsiceros
scrofa *see* Sus
scythica *see* Antilope
seistanica *see* Gazella
setoni *see* Rangifer
severtzovi *see* Capra, Ovis
shantungensis *see* Ovis
sibirica *see* Capra, Cervus
sibiricus *see* Cervus, Ibex, Moschus, Rangifer, Sus
sifanicus *see* Moschus
Sika 100
sika *see* Cervus
Sikaillus 100
silvatica *see* Equus
silvicola *see* Rangifer
Simiae 9
simus *see* Diceros
sinaitica *see* Capra
Sirenia 10, 11
sivalensis *see* Bison
soemmeringei *see* Gazella
sondaicus *see* Rhinoceros
songarica *see* Cervus
songaricus *see* Cervus, Sus
spekei *see* Gazella, Strepsiceros
stenonis *see* Equus
stonei *see* Ovis
storcki *see* Ovis
Strepsiceros 373, 374
— angasi 373
— imberbis 373
— scriptus 373
— spekei 373
— strepsiceros 373
Strepsicerotinae 372
Strepsicerotini 373
Strongylocerus 100
subgutturosa *see* Antilope, Gazella
Suidae *22*, 23, **24**, 25
Suiformes 18, 21, 72, 74
Suina 23, 24, 25
sumatraensis *see* Capricornis
sumatrensis *see* Didermoceros
Suoidea 23
Sus 16, **25**, 26, *26*
— andamanensis 44
— attila 27, **43**, 44
— barbarus 44
— barbatus 26, *26*, 27, 31
— castillanus 44
— celebensis 27
— chirodontus 44
— continentalis 27, 44
— cristatus 27, 44
— europaeus 27
— falz-feini 27, 43, 44
— floresianus 44
— gargantua 27
— gigas 27, 44
— koreanus 45
— leucomystax 27, 44
— lybicus 43, 44
— majori 44
— mandchuricus 44
— meridionalis 44
— moupinensis 45
— nicobaricus 44

— nigripes 27, **43**, 44
— papuensis 45
— raddeanus 27, **44**
— reiseri 44
— riukianus 44
— salvanius 26, 27, 31
— scrofa 25, *26*, **27**, 31, *33*, *37*, *42*, **43**, **44**
— sibiricus 27, **44**
— songaricus 44
— taivanicus 44
— timorensis 44
— ussuricus 27, **44**
— verrucosus **27**
— vittatus 27, **44**
sylvestris *see* Equus
Syncerus 374, 386
— caffer 374
— nanus 374

tafeli *see* Microhippus
taiouanus *see* Cervus
taivanicus *see* Sus
Tajassu 23
Tajassuidae *22*, 23, 25
Tapiridae 690, 695
Tapirus bairdi 691
— indicus 688, 691
— pinchaque 691
Tapirus terrestris 691
Tarandus 299
Tarandus borealis 302
— chukchensis 303, 323
— furcifer 302, 303
— lapponum 302
— lenensis 303
— yakutskensis 303
tarandus *see* Cervus, Rangifer
tarpan *see* Equus
Tarsioidea **9**
tatarica *see* Capra, Saiga
tauricus *see* Cervus
Taurotragus 373, 374
— oryx 373
— euryceros 373
Taurus 374
taurus *see* Bos
taxicolor *see* Budorcas
terraenovae *see* Rangifer
terrestris *see* Tapirus
Tetraceros 16, 362, 371, 372, 373, 374
— quadricornis 373
Thaocervus 99
Theria 10
thomsoni *see* Gazella
tianschanicus *see* Capreolus
tilonura *see* Gazella
timorensis *see* Cervus, Sus
Titanotheriidae 690
tomensis *see* Ovis
Trachelocele **421**, **422**
Tragelaphinae **372**
Tragelaphus **373**
tragocamelus *see* Boselaphus
Tragulidae 71, 72, 74, 364
Tragulina 74
Traguloidea 74, 79, 82
Tragulus 74
tragus *see* Rupicapra
transalaiana *see* Capra
transsylvanicus *see* Capreolus
transuralensis *see* Rangifer
trochoceros *see* Bos
Tubulidentata 10
turcmenicus *see* Capra
Turocapra 517
turovi *see* Moschus
Tylopoda 18, 69, 72, 74
tymensis *see* Alces
typica *see* Capra, Gazella, Ovis
typicus *see* Alces, Cervus, Rangifer

Unguiculata 10
unicolor *see* Cervus
unicornis *see* Rhinoceros
uralensis *see* Alces
Urmiabos 375
urmiana *see* Ovis
Urotragus 485
Urus 374
— nostras 388
— scoticus 374
urus *see* Bison, Bos
ussuricus *see* Elaphus, Sus

Valentinae *see* Rangifer
varenzovi *see* Ovis
verrucosus *see* Sus
vicugna *see* Lama
vignei *see* Ovis
vittatus *see* Sus
vulgaris *see* Capreolus, Cervus

wachei *see* Cervus
walie *see* Capra
wallichi *see* Cervus
warthae *see* Capreolus
weemsi *see* Ovis

xanthopygos *see* Cervus

yakutskensis *see* Alces, Tarandus
yarkandensis *see* Gazella

zdanskyi *see* Ovis
zebra *see* Equus
zedlitzi *see* Capreolus

39088000448746

(v.1)

TT 76-52040